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THE CHACOAN PECCARY
CATAGONUS WAGNERI (RUSCONI)

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CONTENTS

INTRODUCTION

A third species of living peccary (Fig. 1), Tayassuidae, representing a generic addition to the fauna of the Paraguayan Chaco, was announced by Wetzel, Dubos, Martin, and Myers (1975). We assigned this form to the genus *Catagonus* Ameghino, formerly known only from the Lower and Middle Pleistocene of Argentina, and indicated evidence of its close relationship to the genus *Platygonus* LeConte from the Upper Pliocene to postglacial times. We postulated that *Catagonus* occurs in most or all of the Gran Chaco. Since that writing, two skulls of *Catagonus*, collected in 1936 by José Yepes from the Argentine province of Salta, have been identified (Wetzel and Crespo, 1976) and conversations with hunters in the Bolivian Chaco indicate that *Catagonus* also occurs in that nation. [Also *see* Olrog et al (1976)]

The Gran Chaco extends from southeastern Bolivia through western Paraguay and into northwestern Argentina. It is an area of thorn steppe or thorn forest, often with dense and spiny undergrowth. In Paraguay, the Chaco covers an area two-thirds the size of California and is traversed by the Trans-Chaco highway that begins north of Asunción and runs northwesterly to the Bolivian border. Rainfall decreases from 1400 mm per year in the palm savannah of the Paraguay River valley to 400 mm per year along the western border of Paraguay, where grasses and bare sand occur between the more scattered trees and shrubs. The landscape is virtually flat, broken by extensive grass and palm swamps in areas of higher rainfall and by a few permanent and numerous intermittent streams (*see* Wetzel and Lovett, 1974; Short, 1975). Western Paraguay occupies three-fifths of the nation, but has only 4% of the population. Except for the Mennonite farming communities around Filadelfia, the Paraguayan Chaco contains large ranches, occasional small army posts, and much unused land. Several different derivations of the word *Chaco* have been postulated, but an appropriate one is that it comes from the Quechuan *chacu,* meaning an abundance of animal life (Weil et al., 1972). José de Acosta stated that *chaco* was a method of hunting by encirclement, and Garcilaso de la Vega used *chacu* to mean the annual ceremonial hunt of the Incas, in which encirclement was the method of capture (Barbara G. Beddall, pers. commun.).

Zoogeographical studies that mention the Chaco have been largely without benefit of recent studies of its mammalian fauna. The more recent continental analyses treat the Gran Chaco as follows: Hershkovitz (1972) grouped the Chaco with other adjacent faunal areas as a Paraná-Paraguay Valley District, a transitional zone between the Brazilian and Patagonian Subregions. Fittkau (1969) placed the Chaco on the boundary between the Guiana-Brazilian and the Andean-Patagonian Regions, but fragmented it among three extensive zoogeographic provinces. Müller (1973:143-145), after considering the overlap of northern and southern faunas, found sufficient endemic animal species and subspecies to designate a separate Chaco Center. He grouped (p. 175) the Chaco with nonforest dispersal centers that he considered to have alternately expanded in arid periods and contracted during moist periods of the Quaternary. Other recent authors who have summarized the evidence for this ebb and flow of xeric vs. mesic habitats and their biota during Quaternary glacial-interglacial cycles include Eden (1974), Haffer (1974), Van der Hammen (1974), Short (1975), and Fairbridge (1976). Blair (1976) compared the anurans of the Sonoran of North America, the Chaco, and the Monte. The data he reviewed for the Chaco were restricted to Argentina, and his use of the term Chaco was much broader than the use in this paper. Solbrig (1976) wrote that Cabrera (1971) designated one of his three principal floral divisions of Neotropical South America as the Chaco Dominion, and one of its seven subdivisions as the Chaco Province. It is this latter use, except for restricting the eastern border of the Chaco to the Río Paraguay, that I follow here.

Prior to our report of the Chacoan peccary, *Catagonus* was restricted to two extinct species. Ameghino (1904) named the genus *Catagonus* when he described *C. metropolitanus,* based on a palate in two fragments, from Lower Pleistocene deposits in the city of Buenos Aires. In the same paper he described from the Middle Pleistocene of Buenos Aires *Listriodon bonaerensis,* based on isolated teeth, and this species was later moved to the genus *Catagonus* by Rusconi (1930).

LeConte (1848) described *Platygonus* from the North American Upper Pleistocene, and several species have been described from South American deposits. Among these, Rusconi (1930) described *Platygonus (Parachoerus) carlesi* from Middle Pleistocene deposits near the Río Dulce in Santiago del Estero, western Argentina. *Platygonus carlesi wagneri* Rusconi (ibid.) was reported in association with pre-Hispanic funeral urns, artifacts, and a large modern mammalian fauna from the vicinity of Melero in Santiago del Estero (Fig. 2). Rusconi (1948) later raised *wagneri* to the level of species. Both *P. carlesi*
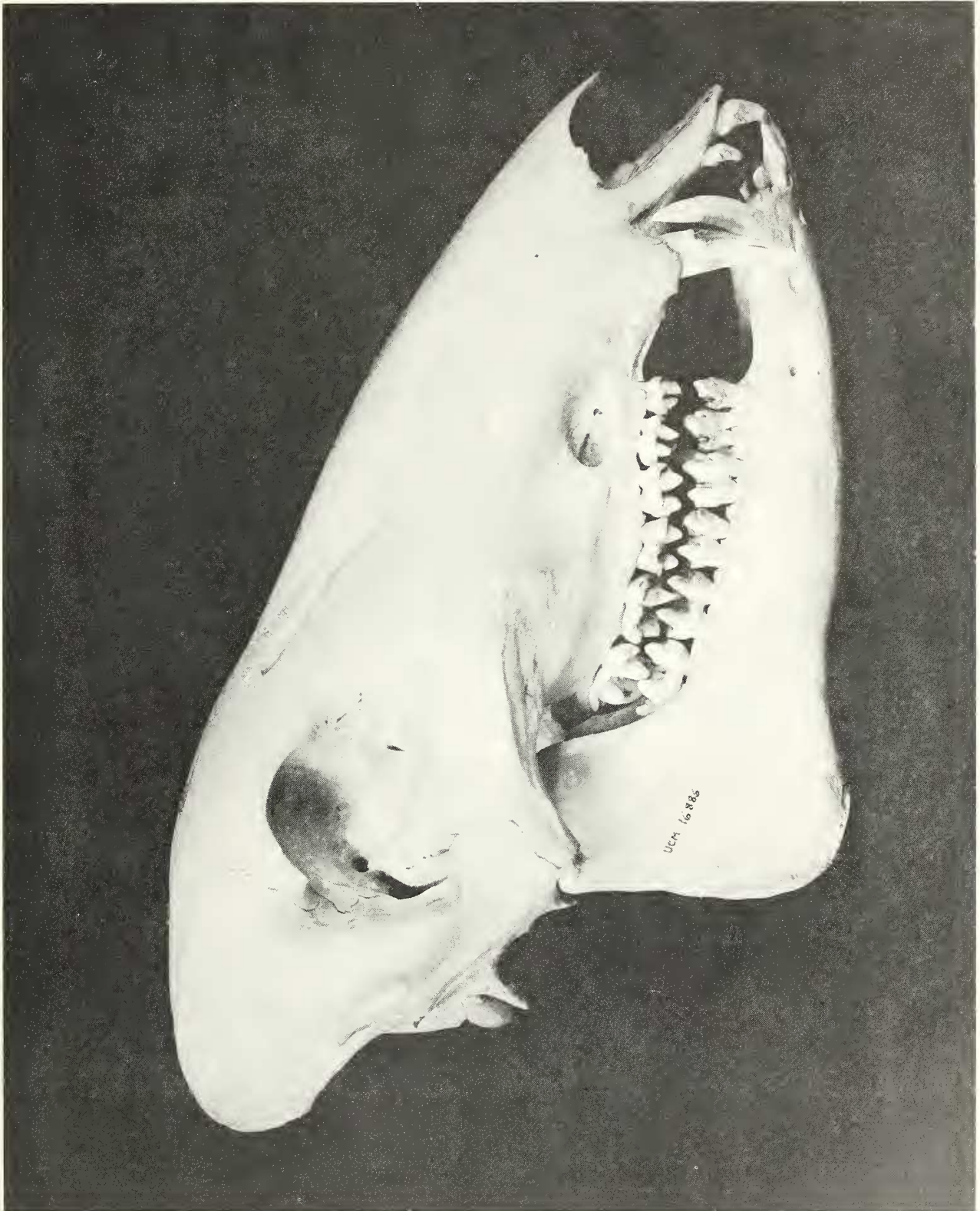
Fig. 1. Skull of the Chacoan peccary or Taguá, *Catagonus wagneri* (Rusconi). Specimen is CONN 16886, collected 10 km W Fortín Teniente Montania, Depto. Boquerón, Paraguay, 21 July 1974.
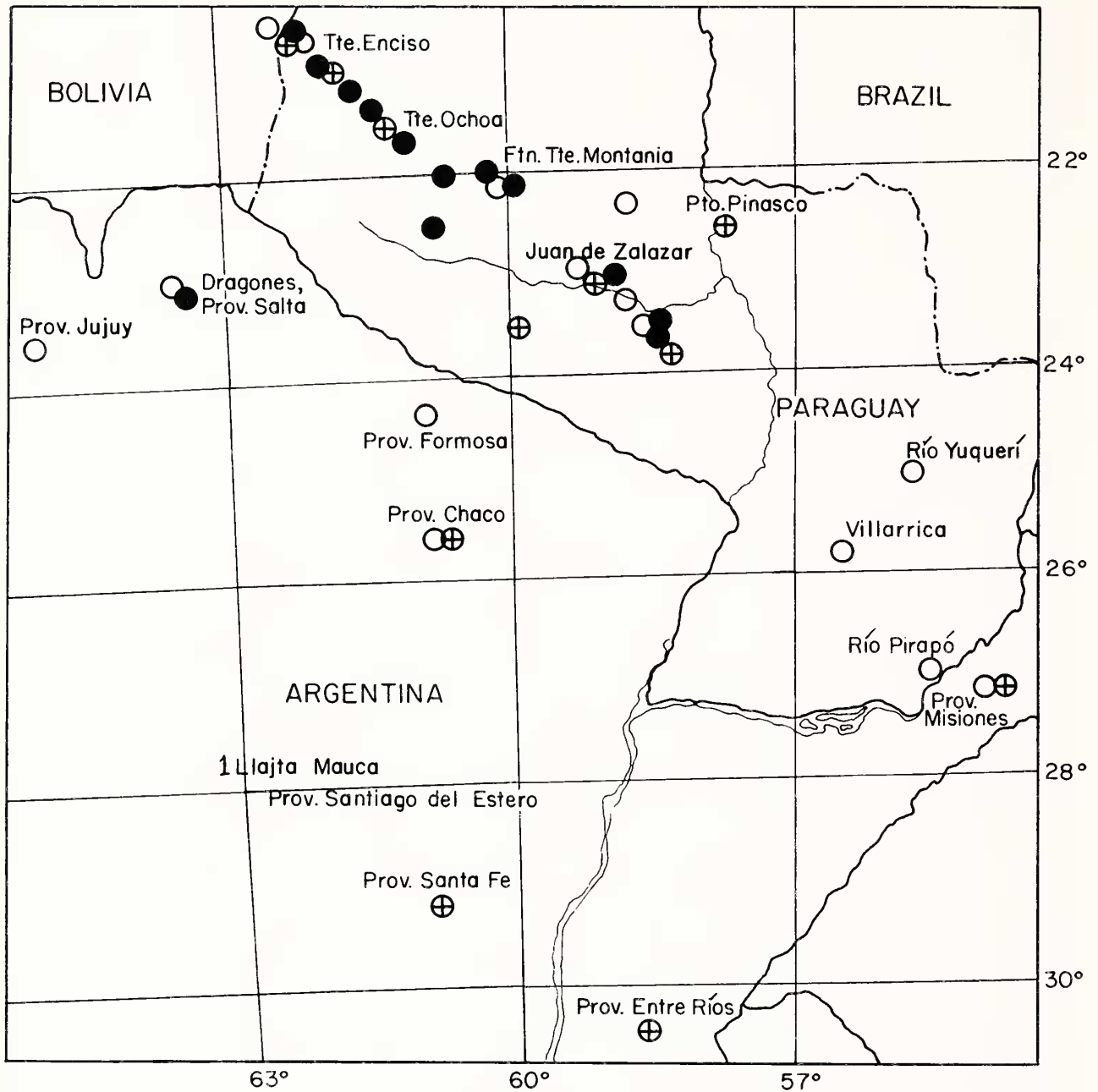
Fig. 2. Provenance of Recent peccary specimens examined. ● *Catagonus wagneri*. ⊕ *Tayassu pecari*. ○ *Tayassu tajacu*. **1**, type-locality, *C. wagneri* (Rusconi 1930, 1948).

and *P. wagneri* were based upon complete or nearly eomplete crania.

The Chacoan peccary proved to be conspecific with *P. wagneri*. Despite the similarities of this species and *P. carlesi* to North American *Platygonus,* the molari-form premolars and larger molars were distinct from all the *Platygonus* examined. *P. carlesi* and *P. wagneri,* in fact, were nearer to *Catagonus metropolitanus* and *C. bonaerensis* and were considered congeneric (Wetzel et al., 1975). I have since examined *Platy-gonus rebuffoi* Rusconi (1952), based upon a partial mandible, from the Middle Pleistocene of Uruguay

and find it assignable to the genus *Catagonus*. Thus all the species placed in the subgenus *Parachoerus* Rusconi belong, in my view, to the genus *Catagonus*.

In the Chaco, *Catagonus wagneri* is distinguished from the other living peccaries by any one of a number of Guaraní or Spanish names, e.g., Paguá, Taguá, or Curé-buro. The white-lipped peccary, *Tayassu pecari* (Link), is there known as Tagnicate or Tâchy-câtí, and the collared peccary, *T. tajacu* (L.), as Tayté-tou or Cure-í. The Recent specimens of *C. wagneri* are here described in more detail than was possible in the first brief report, and are contrasted with *T. pecari* and *T. tajacu* from Paraguay and adjacent Argentina. During the course of this study, such repeated comparisons have strongly emphasized the much closer relationship of *T. pecari* and *T. tajacu*. I am therefore abandoning Woodburne's (1968) generic separation into *T. pecari* and *Dicotyles tajacu,* and returning to a congeneric treatment of those two species. Detailed comparisons of the crania of *T. pecari* and *T. tajacu* may be found in both Rusconi (1929) and Woodburne (1968), and comparisons of those two species with *Platygonus compressus* in Guilday, Hamilton, and McCrady (1971). Such comparisons are therefore not repeated here. Comparisons with fossil forms are restricted to those assigned to the genera *Catagonus, Platygonus,* and, for comparative purposes, samples of *Prosthennops* Gidley and *Mylohyus* Cope. The genus *Selenogonus* Stirton (1947) from the Upper Pliocene or Pleistocene of Colombia is not included in the comparisons,

and I have avoided a definite stand on the genus *Argyrohyus* Kraglievich (1959) from the Upper Pliocene of Argentina. Neither holotype was examined, and the limited information in the descriptions, because of the fragmentary nature of the specimens, dictates restraint in commenting on those important specimens. I use *Platygonus marplatensis* Reig (1952), rather than *Argyrohyus chapadmalensis* (Castellanos) which Kraglievich considered the senior synonym. This is both a convenience and a bias on my part. In the use of *Platygonus chapadmalensis* (Ameghino) for another specimen (MMCN 246) in the collection at Mar del Plata, I have followed Reig.

In June 1975, during a visit to the Museo Argentina de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, the holotype of *C. bonaerensis* was photographed and measured. Unfortunately, the holotype of *C. metropolitanus* has been lost. Hereinafter, measurements of *C. metropolitanus* are from Rusconi (1930). Rusconi's holotypes of *C. wagneri* and *C. carlesi* have not as yet been located. Measurements in this paper, therefore, are from Rusconi (1930, 1948). Most measurements for *P. compressus* from Welsh Cave, Kentucky, are from Guilday et al. (1971). When my measurements of this species are given, the number of specimens is always indicated. Measurements of crania, teeth, and metapodials of *C. wagneri* from the Chaco of Paraguay are listed in Table 1 and may be compared with Rusconi's measurements of his holotypes and with Guilday's measurements of *P. compressus*.

ACKNOWLEDGMENTS

Table 1. Skeletal measurements, *Catagonus wagneri*, Chaco of Paraguay.

Measurement	$\bar{Y}$	s	C	O.R.	N
Cranita with adult dentition					
Greatest length	309.9	6.7	2.2	298-324	29
Condylobasal length (CBL)	266.6	7.2	2.7	252-280	27
Basal length	255.7	7.4	2.9	241-268	26
Anterior border of orbit to anterior					
of premaxilla (RL)	199.1	5.2	2.6	191-209	31
Postrostral length (CBL-RL adj. = PRL)	71.4	4.1	5.8	62.6-77.0	27
Anterior border of orbit to margin					
of infraorbital foramen	86.7	3.6	4.1	81.1-97.4	31
Zygomatic breadth	125.6	5.7	4.5	108-137	25
Depth of suborbital zygoma	30.3	2.3	7.6	26.0-35.2	30
Depth of zygoma: postorbital process					
of zygoma to preglenoid process	56.0	2.7	4.8	50.9-61.0	24
Vertical diameter of orbit	35.8	1.0	2.8	33.4-37.7	31
Width across canines	60.5	2.4	4.0	55.8-65.7	28
Width across canine buttresses	64.3	2.4	3.8	60.5-69.2	27
Width, maximal, across molar rows	64.4	3.0	4.7	59.0-74.0	27
Width, minimal, between P^2's	27.2	2.0	7.2	22.7-32.4	29
Width, minimal, between M^2's	24.7	1.9	7.6	20.8-29.9	30
Width, minimal, between orbits	77.5	4.1	5.3	70.0-89.0	30
Width across postorbital processes	100.4	3.9	3.9	93-109	29
Length of precanine diastema	20.1	2.3	11.6	13.3-26.3	31
Length of postcanine diastema	23.9	3.2	13.4	18.8-29.1	31
Height of nasal opening	31.2	1.2	3.8	29.0-33.3	23
Height of occiput from ventral border					
of condyles	100.4	4.2	4.2	93-109	26
Width across occipital condyles	43.6	1.6	3.5	40.1-46.1	26
Cranial capacity	114.1	7.9	6.9	102-130	22
Mandibles with adult dentition					
Length, condyle to tip	209.8	5.7	2.7	200-222	20
Height, maximal, posterior	93.0	3.5	3.7	86-99	20
Width, maximal, posterior	109.8	7.2	6.6	99-122	21
Length of postcanine diastema	30.8	4.1	13.4	21.4-36.4	23
Depth below middle of postcanine diastema	23.4	1.4	6.0	20.2-25.3	23
Depth below anterior margin of M_1	31.2	1.8	5.8	25.8-33.6	23
Length of symphysis	56.2	3.2	5.7	47.4-61.8	21
Deciduous dentition					
dP^{2-4}, length	33.3	----	----	----	1
dP^2, length	9.2	----	----	----	1
width	7.5	----	----	----	1
dP^3, length	11.6	----	----	11.1, 12.2	2
width	11.2	----	----	10.3, 12.2	2
dP^4, length	13.3	----	----	13.1-13.7	3
width	12.4	----	----	12.1-12.7	3
dP_{2-4}, length	34.8	----	----	34.1-35.3	4
dP_2, length	7.4	----	----	6.7-7.8	4
width	4.0	----	----	3.9-4.0	5
dP_3, length	9.8	----	----	9.6-10.2	5
width	6.4	----	----	6.1-6.6	5
dP_4, length	18.2	----	----	17.7-18.9	5
width	10.4	----	----	10.2-10.5	5

Table 1. Skeletal measurements, *Catagonus wagneri*, Chaco of Paraguay (continued).

Measurement	$\bar{Y}$	s	C	O.R.	N
			Permanent dentition		
P^2-M^3, length	94.8	2.6	2.7	91.0-99.1	23
P^{2-4}, length	38.2	1.9	5.0	32.1-41.3	26
M^{1-3}, length	57.9	2.5	4.4	52.7-64.9	27
Upper canine, anteroposterior diameter	15.1	1.0	6.5	13.5-17.3	24
transverse diameter	10.4	0.8	7.7	9.0-12.2	23
P^2, length	11.4	0.6	5.6	10.1-12.8	29
width	9.6	0.7	7.1	8.4-11.1	29
P^3, length	13.2	0.8	6.0	11.5-14.8	34
width	13.1	0.7	5.2	12.1-14.6	33
P^4, length	15.0	0.8	5.6	13.1-17.8	36
width	15.2	0.8	5.3	13.6-16.9	36
M^1, length	16.6	1.0	5.9	14.7-18.4	38
width	15.4	0.7	4.5	14.0-16.9	37
M^2, length	20.6	0.9	4.5	18.7-22.5	37
width	18.8	1.0	5.1	17.0-20.9	37
M^3, length	22.3	1.3	5.9	20.1-25.4	28
width of anterior moiety	18.9	1.0	5.3	16.5-20.6	27
width of posterior moiety	17.4	0.8	4.3	16.1-18.6	28
P_2-M_3, length	98.7	3.8	3.8	90.5-107.6	16
P_{2-4}, length	37.4	2.0	5.4	32.8-41.5	16
M_{1-3}, length	61.9	2.0	3.2	58.0-66.7	21
Lower canine, anteroposterior diameter	15.4	0.9	5.7	13.7-17.0	18
transverse diameter	10.5	0.7	6.8	9.0-11.7	18
P_2, length	9.3	0.6	6.4	7.8-10.1	15
width	5.9	0.5	7.7	5.4-6.8	15
P_3, length	12.6	0.6	5.1	11.3-14.0	19
width	8.8	0.5	5.4	8.1-9.8	19
P_4, length	16.2	1.0	6.2	14.4-19.4	22
width	12.6	0.6	5.1	11.4-13.8	22
M_1, length	17.0	0.9	5.4	15.2-18.8	28
width	13.0	0.5	3.9	11.9-13.9	28
M_2, length	20.5	1.0	4.7	18.7-22.3	28
width	16.5	0.6	3.8	15.1-17.8	27
M_3, length	26.2	1.6	6.0	24.3-30.6	21
width of anterior moiety	16.4	0.8	5.1	14.9-18.1	21
width of posterior moiety	15.9	0.6	3.8	14.4-16.8	21
			Length of metapodials		
Metacarpal II	41.5			39.8-44.4	4
III	67.4			65.1-70.5	5
IV	69.8			68.5-71.4	5
V	52.6			50.3-53.7	5
Metatarsal II	47.2			43.6-51.2	4
III	80.0			79.0-81.5	5
IV	82.4			81.5-83.4	5
V	48.6			46.0-50.4	5

At this University, Robert E. Dubos measured many of the skulls with me, John J. Mayer noted the similarity to *Platygonus,* Theodore A. Heist adapted data for computer analysis, Mary Hubbard and her staff prepared the figures, Adelaide Ellsworth and Robert Pirozok sectioned hairs, and Solomon E. Wollman photographed the skull and toothrows.

I am especially indebted to the following institutions and curators who generously permitted examination of specimens under their care. The following abbreviations are used in later accounts to identify the location of specimens:

AMNH—The American Museum of Natural History, New York, Malcolm C. McKenna.

BMNH—British Museum (Natural History), London, G. B. Corbet.

CM—Carnegie Museum of Natural History, Pittsburgh, Mary R. Dawson.

CONN—The University of Connecticut Museum of Natural History, Storrs.

MACN—Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Guillermo del Corro and Jorge A. Crespo.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Barbara Lawrence.

MDC—Museo Departmental de Colonia, Uruguay, Bautista Rebuffo.

MHN—Museo de Historia Natural, Universidade Federal de Minas Geraís, Belo Horizonte, José Silvio Fonseca.

MMCN—Museo Municipal de Ciencias Naturales, Mar del Plata, Galileo J. Scaglia.

MN—Museu Nacional, Rio de Janeiro, Fernando D. de Avila-Pires and Fausto L. de Souza Cunha.

MNHN—Museo Nacional de Historia Natural, Montevideo, Alvaro Mones and Alfredo Ximénez.

MU[1]—The Museum, Texas Tech University, Lubbock, Patricia Vickers Rich.

MVZ—Museum of Vertebrate Zoology, University of California, Berkeley, J. L. Patton.

TMM—Texas Memorial Museum, University of Texas, Austin, Ernest L. Lundelius, Jr.

USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C., Charles O. Handley, Jr. and Clayton E. Ray.

SPECIMENS EXAMINED

Collection sites along the Trans-Chaco highway of Paraguay are given in kilometers (Km) from the beginning of the road at Villa Hayes, northeast of Asunción. Lower case (km) is used for distances from other points. Numbers preceding abbreviations for museums indicate the number of specimens examined. Numbers following such abbreviations are museum accession numbers.

Catagonus wagneri, Recent—56 (Fig. 2). ARGENTINA. Salta: 1 MACN, unspecified locality; 1 MACN, Dragones. PARAGUAY. Boquerón: 4 CONN, 28-40 km N Filadelfia, road to Fortín Teniente Montania; 5 CONN, 10-42 km W Ftn. Tte. Montania, road to Mariscal Estigarribia; 1 CONN, Km 480; 1 CONN, Km 530; 1 CONN, Ftn. Capitán O. Serebriakof. Nueva Asuncíon: 12 CONN, Km 555-607, vicinity of Tte. Ochoa; 24 CONN, Km 613-667, vicinity of Tte. Enciso; 2 CONN, Km 764, Ftn. Sgto. Rodriguez (Villazón). Presidente Hayes: 3 MVZ, Km 275; 1 CONN, Km 277.

Catagonus spp., fossil. ARGENTINA. Buenos Aires: MMCN 41, NNE Mar del Plata (Miramar Form., Ensenadense, Mid-Pleistocene); MMCN 707, Cuidad de San Antonio de

Areco ("Bonaerense?," Mid-Pleistocene?); MMCN 972, Ayo. Lobería (Barranca Lobos Form., inf., Lower Pleistocene). Distrito Federal: MACN 2440, *L. bonaerensis* Ameghino, holotype (Bonaerense, Mid-Pleistocene). URUGUAY. Colonia: MDC 1345, *P. rebuffoi* Rusconi, holotype, 50 km N Colonia del Sacramento (Bonaerense, Mid-Pleistocene).

Platygonus spp. ARGENTINA. Buenos Aires: MMCN 25, *P. marplatensis* Reig, holotype, Barranca de Los Lobos, 1 km NE Baliza Caniú (layer 3, Chapadmalal Form., Montehermosense, Upper Pliocene); MMCN 156, *P. scagliae* Reig, holotype, Chapadmalal (Barranca de Los Lobos Form., Vorhué inf., Uquiense, Lower Pleistocene); MMCN 246, Punta San Andrés (Vorhué inf., Uquiense, Lower Pleistocene); MMCN 878, SW Ayo. Lobería (Barranca de Los Lobos Form., Uquiense, Lower Pleistocene); MMCN 1212, Cañada Chapar (Vorhué inf., Lower Pleistocene). BRAZIL. Minas Gerais: 3 MHN, caves (Pleistocene-subRecent). MEXICO. Guanajuato: 1 USNM, *P. alemanii* Dugès, holotype, Moroleón (Pleistocene). UNITED STATES. Arizona: 4 AMNH, Papago Springs (Rancholabrean). Florida: 1 USNM, Melbourne (Pleistocene). Idaho: 1 USNM, Hagerman Form. (Hemphillian). Kansas: 9 AMNH, Edson Quarry (Hemphillian). Kentucky: 15 CM, Welsh Cave (Rancholabrean). Maryland: 8 USNM, *P. cum-*

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[1]The symbol TTU-P was inadvertently not used to indicate the paleontological collection of The Museum, Texas Tech University.

berlandensis Gidley, incl. holotype, Cumberland Cave (Irvingtonian). Missouri: 7 AMNH, Cherokee Cave (Rancholabrean). Nebraska: 1 AMNH, Snake Creek Form. (Hemphillian). Tennessee: 5 CM, Guy Wilson Cave (Rancholabrean). Texas: 2 MU, Carter Quarry (Blancan); 3 TMM, Crosby Co. (Blancan); 1 AMNH, Channing area ("Hemphillian-Blancan").

Prosthennops spp. UNITED STATES. California: 1 AMNH, Eden (late Hemphillian). Florida: 1 AMNH, Mixon Bone Bed (late Hemphillian). Nebraska: 1 AMNH, Snake River (Valentinian, Lower Pliocene); 3 AMNH, Ash Hollow Form. (late Clarendonian, Lower Pliocene). URUGUAY. Colonia: MDC 398, ?*Prosthennops uruguayensis* Rusconi, holotype, 12 km N Colonia del Sacramento (Pampean Form., Belgranense, Mid-Pleistocene).

Mylohyus spp. UNITED STATES. Arkansas: 1 AMNH, Conard Fissure (Irvingtonian). Florida: 1 AMNH, Seminole Field (Rancholabrean).

Tayassu pecari, Recent—37 (Fig. 2). ARGENTINA. Chaco: 2 MACN, unspecified locality. Entre Ríos: 1 BMNH, unspecified locality. Misiones: 3 MACN, unspecified locality.

Santa Fe: 1 MACN, unspecified locality. PARAGUAY. 1 MNHN, unspecified locality. Nueva Asunción: 3 CONN, Tte. Enciso; 1 CONN, Garrapatel-í, 7 km SW Km 620; 1 CONN, Km 592; 6 CONN, Ftn. Sgto. Rodriguez. Presidente Hayes: 13 CONN, Juan de Zalazar; 1 CONN, Km 194; 1 MVZ, Km 275; 2 USNM, Pto. Pinasco; 1 CONN, 85 km W Pozo Colorado, 10 km N road to Ftn. Ávalos Sánchez.

Tayassu tajacu, Recent—59 (Fig. 2). ARGENTINA. Chaco: 1 MACN, unspecified locality. Formosa: 1 MACN, unspecified locality. Jujuy: 1 BMNH, 1 MACN, unspecified localities. Misiones: 5 MACN, unspecified localities. Salta: 16 MACN, Dragones; 1 MACN, Urundel. BOLIVIA. Chuquisaca: 1 CONN, 8 km E Santa Rosa. PARAGUAY. Boquerón: 4 CONN, 29 km N Filadelfia, road to Ftn. Tte. Montania. Caaguazú: 2 MCZ, Río Yuquerí. Guairá: 2 BMNH, Villarrica. Itapúa: 1 CONN, Pto. Pirapó. Nueva Asunción: 1 CONN, Km 750, Ftn. Gral. E. A. Garay; 5 CONN, Km 764, Ftn. Sgto. Rodriguez; 1 CONN, Km 607; 3 CONN, Tte. Enciso. Presidente Hayes: 3 CONN, Estancia-í, 100 km E Filadelfia; 7 CONN, Juan de Zalazar; 3 MVZ, Km 275.

MEASUREMENTS AND SYMBOLS

All linear measurements, given in millimeters, were taken with dial calipers accurate to .1 and, for the larger dimensions, with GPM calipers accurate to 1. The cranial measurements used in Table 1 and elsewhere include most of those used by Guilday et al. (1971) and Rusconi (1930, 1948) plus the following additions and derivations:

Height of nasal opening: Distance from the most anterior point of nasal bone to midline of dorsal surface of premaxilla, in a line at right angles to the toothrow.

Cranial capacity: An estimate, given in milliliters, of the volume of brain cavity, based upon volume of small beans required to fill the cavity.

Rostral length (RL): Distance from anterior tip of premaxilla to anterior margin of orbit.

Rostral length, adjusted (RL adj.): Distance from

anterior tip of premaxilla, along midline axis of skull, to a line between the anterior margins of orbits. RL adj. is derived as the altitude of a triangle in which RL is the hypotenuse and one-half the interorbital width is the base.

Postrostral length (PRL): Distance from anterior margin of orbits, along the midline axis, to a line across the posterior margin of occipital condyles. PRL is derived as the difference between condylo-basal length and RL adj.

Symbols used in the Tables and elsewhere refer to: $\bar{Y}$ = mean or $\bar{X}$; s = standard deviation of the sample (S.D. of Simpson, 1949 and Guilday et al., 1971); C = coefficient of variation computed as $s/\bar{Y}$ (V of Simpson and of Guilday); O.R. = observed range; N = number in sample.

RELATIVE AGE OF SPECIMENS

Following Herring's (1974) method, I rated the degree of closure of 22 cranial sutures for 45 *C. wagneri,* 21 *T. pecari,* and 20 *T. tajacu,* all CONN specimens from Paraguay. The relative sequence of closure of these sutures within each species was then compared by mean suture fusion scores and by plotting suture closure against age categories. Arbitrary age categories

were based upon the following chronology of tooth eruption and wear. These age categories were applied to all three species, but the following sequence of suture closure is for *C. wagneri.*

0. Immature: Only deciduous teeth in place; no molars present.

1. Young juvenile: Deciduous premolars and first

molar in place. Sutures closed by end of period: inter-parietal and occipito-parietal.

2. Juvenile: Deciduous premolars and first two molars in place. Sutures closed by end of period: interfrontal and intermaxillary; sutures beginning to close: naso-frontal and occipitals.

3. Young adult: Permanent premolars and first two molars in place. Additional sutures closed by end of period: basispheno-occipital, naso-frontal, and occipitals; sutures beginning to close: fronto-parietal, internasal, interpremaxillary, jugo-frontal, maxillo-frontal, maxillo-jugal, naso-maxillary, occipito-squamosal, premaxillo-maxillary, premaxillo-nasal.

4. Adult: Third molar in place, but without wear. Additional sutures closed by end of period: fronto-parietal, internasal, interpremaxillary, jugo-frontal, maxillo-frontal, maxillo-jugal, naso-maxillary, occipito-squamosal, premaxillo-maxillary; sutures beginning to close: alispheno-squamosal, basispheno-presphenoid, jugo-squamosal, maxillo-alisphenoid, parieto-squamosal.

5. Adult: Moderate wear on first and second molars, slight wear on third molar. Additional sutures closed by end of period: alispheno-squamosal, jugosquamosal, maxillo-alisphenoid, parieto-squamosal, premaxillo-nasal.

6. Adult: Moderate to heavy wear on first two molars, moderate wear on last molar. Additional suture closed before end of period: basispheno-presphenoid.

7. Old adult: Molars worn to basins.

COMMENTS: The sequence of eruption of premolars and molars proved to be the same in all three species. The age at which teeth erupted is not known for *C. wagneri* nor *T. pecari*. Kirkpatrick and Sowls (1962) determined the sequence and time of tooth eruption in 26 captive *T. tajacu* in Arizona. In that species the first two upper molars were present by 43 (37-50) weeks of age, the permanent upper premolars by 72 (66-83) weeks, and the last upper molars by 83 (74-94) weeks; there was no significant difference between upper and lower dentition.

The relative sequence of closure of cranial sutures is indicated in Table 2 for the three peccaries as mean suture fusion scores and as the sequence of closures within each species. As the samples for this comparison are restricted to CONN specimens from Paraguay and all but one specimen, *T. tajacu* from southeastern Paraguay, are from the Chaco, any possible effect of geographical variation upon sequence of closure has been reduced. This geographical homogeneity and some dissimilarity in sutures chosen for scoring may explain variation between the differences found by Herring (1974) for the species of *Tayassu* and the differences found in my study. The major differences found here, however, are between *C. wagneri* on one hand and the two species of *Tayassu* on the other. Of 22 sutures rated, 18 differed from *Tayassu* by more than .1 fusion score and one closure rank or more. Seven of the 22 sutures closed earlier and 10 sutures closed later than in *T. pecari* and *T. tajacu*. Fusion scores for internasal and basispheno-presphenoid sutures differed from the other species by more than .2 but fell between the scores of the two *Tayassu*. For the remaining three sutures scored, the fusion score in *C. wagneri* was similar to *T. tajacu* for occipito-parietal and similar to *T. pecari* for interpremaxillary and basispheno-occipital.

SYSTEMATIC ACCOUNT
Catagonus Ameghino

Catagonus Ameghino, 1904:188; Rusconi, 1930:164; Wetzel et al., 1975.

TYPE SPECIES: *C. metropolitanus* Ameghino, *loc. cit.* Holotype not at MACN, June 1975. Ensenadense, Mid-Pleistocene, Argentina, Buenos Aires.

Listriodon bonaerensis Ameghino, 1904:186. Holotype: MACN 2440. Bonaerense, Mid-Pleistocene, Argentina, Buenos Aires.

Platygonus (Parachoerus) carlesi Rusconi, 1930:150. Holotype not at MACN, June 1975. Bonaerense, Mid-Pleistocene, Argentina, Santiago del Estero, Las Termas, Río Dulce.

Catagonus (Interchoerus) bonaerensis.—Rusconi, 1930:168, based upon Ameghino, 1904:186.

Platygonus (Parachoerus) carlesi wagneri Rusconi, 1930:231 and *Platygonus wagneri.*—Rusconi, 1948:231. Pre-Hispanic deposits, Argentina, Santiago del Estero, Llajta Mauea.

Platygonus (Parachoerus) rebuffoi Rusconi, 1952:125; Mones and Francis, 1973:77. Holotype: MDC 1345. Bonaerense, Mid-Pleistocene, Uruguay, Colonia, Arroyo de Las Limetas.

RANGE OF CATAGONUS: Lower Pleistocene of Argentina and Uruguay to Recent of Gran Chaco.

COMPARISONS: The skull of *Catagonus* (Fig. 1) is similar to *Platygonus* and differs from *Tayassu* (including *Dicotyles*) in having extreme development of the rostrum, nasal chamber, and sinuses; braincase

proportionally and often actually smaller; infraorbital foramen well anterior to zygomatic arch; pronounced articular fossa absent on anterior face of zygomatic arch; zygomatic bar below orbit deeper; orbits more posterior in position, anterior edge of orbit well posterior to last molar, and postorbital process of zygomatic well posterior to preglenoid process; pronounced basicranial flexure; teeth hypsodont; and molars with four major cusps.

Cranial characters of *Catagonus* that distinguish it from *Platygonus* (Fig. 3) are: molars larger, toothrows longer; postcanine diastemas shorter; premolars and molars with cuspules; last premolars (P^4 molariform, with four major cusps vs. two cusps; cingula well developed on most premolars and molars, complete on buccal side of all upper premolars and molars; lower first premolar (P_2) with a single major cusp (Fig. 4) vs. paired lateral cusps; last upper molar (M^3) quadrangular, lacking a pronounced posterior constriction in transverse width. Excepting the earliest forms of *Platygonus, Catagonus* also differs in having three pairs of lower incisors and a more gracile skull that lacks the flared zygomata and keeled genium.

Catagonus is similar to *Prosthennops* in that the last premolars are molariform, but differs from the latter in having larger molars with cingula more completely developed, longer toothrows, and shorter postcanine diastemas. A more definitive separation of *Prosthennops* (with the latest occurrence in the Upper Pliocene) from *Catagonus*, which was first known from the Lower Pleistocene, awaits a better understanding of the upper limits of *Prosthennops*.

Catagonus differs from *Platygonus* (*Brasiliochoerus* Rusconi, 1930) in having the M^3 larger than M^2, particularly for the anteroposterior diameter. *Brasiliochoerus* is unusual among the Pliocene-to-Recent tayassuids of North and South America in having the M^3 smaller than M^2 for both anteroposterior and transverse diameters, as shown in Table 3. The remaining characters presented by Rusconi are not unique to *Brasiliochoerus*: (1) The features of molariform premolars and the P^4 with four main cusps and nearly the same size as M^1 are shared by *Catagonus, Brasiliochoerus, Prosthennops* and *Mylohyus*. (2) A glenoid fossa ventral to the orbit and, although not listed by Rusconi, an anterior opening of the infra-

Table 2. Comparison of mean suture fusion scores* and sequence of closure of cranial sutures for the three species of Recent peccaries. Suture fusion scoring follows Herring (1974): 0 = unfused, 1 = less than half fused, 2 = about half fused, 3 = more than half fused, and 4 = completely fused.

Cranial suture	C. wagneri		T. pecari		T. tajacu	
interparietal	3.98	1st	3.46	2nd	3.40	2nd
occipito-parietal	3.95	2nd	3.63	1st	3.92	1st
interfrontal	3.89	3rd	3.46	2nd	3.40	2nd
occipitals	3.82	4th	3.39	7th	3.23	5th
intermaxillary	3.64	5th	3.46	2nd	3.40	2nd
naso-frontal	3.58	6th	3.46	2nd	3.22	6th
occipito-squamosal	3.50	7th	1.72	21st	2.28	17th
premaxillo-maxillary	3.16	8th	3.46	2nd	3.22	6th
internasal	3.11	9th	3.37	8th	2.93	14th
interpremaxillary	3.07	10th	3.04	14th	2.86	15th
naso-maxillary	2.98	11th	3.24	9th	3.22	6th
fronto-parietal	2.96	12th	2.83	15th	2.79	16th
basispheno-occipital	2.85	13th	2.80	16th	3.12	11th
premaxillo-nasal	2.80	14th	3.24	9th	3.08	12th
maxillo-frontal	2.78	15th	3.12	11th	3.22	6th
jugo-frontal	2.73	16th	3.07	13th	3.03	13th
maxillo-jugal	2.49	17th	3.16	11th	3.17	10th
maxillo-alisphenoid	1.86	18th	2.33	18th	2.18	19th
alispheno-squamosal	1.67	19th	1.82	20th	1.90	21st
jugo-squamosal	1.62	20th	1.95	19th	2.22	18th
basispheno-presphenoid	1.62	20th	1.16	22nd	1.99	20th
parieto-squamosal	1.58	21st	2.50	17th	1.90	21st

*Original mean suture fusion scores for entire samples: *C. wagneri*, 2.893; *T. pecari*, 3.188; *T. tajacu*, 2.915. The following constants were applied to adjust *Tayassu* samples to a mean age equivalent to that of *Catagonus* sample: *T. pecari*, .9075; *T. tajacu*, .9923.
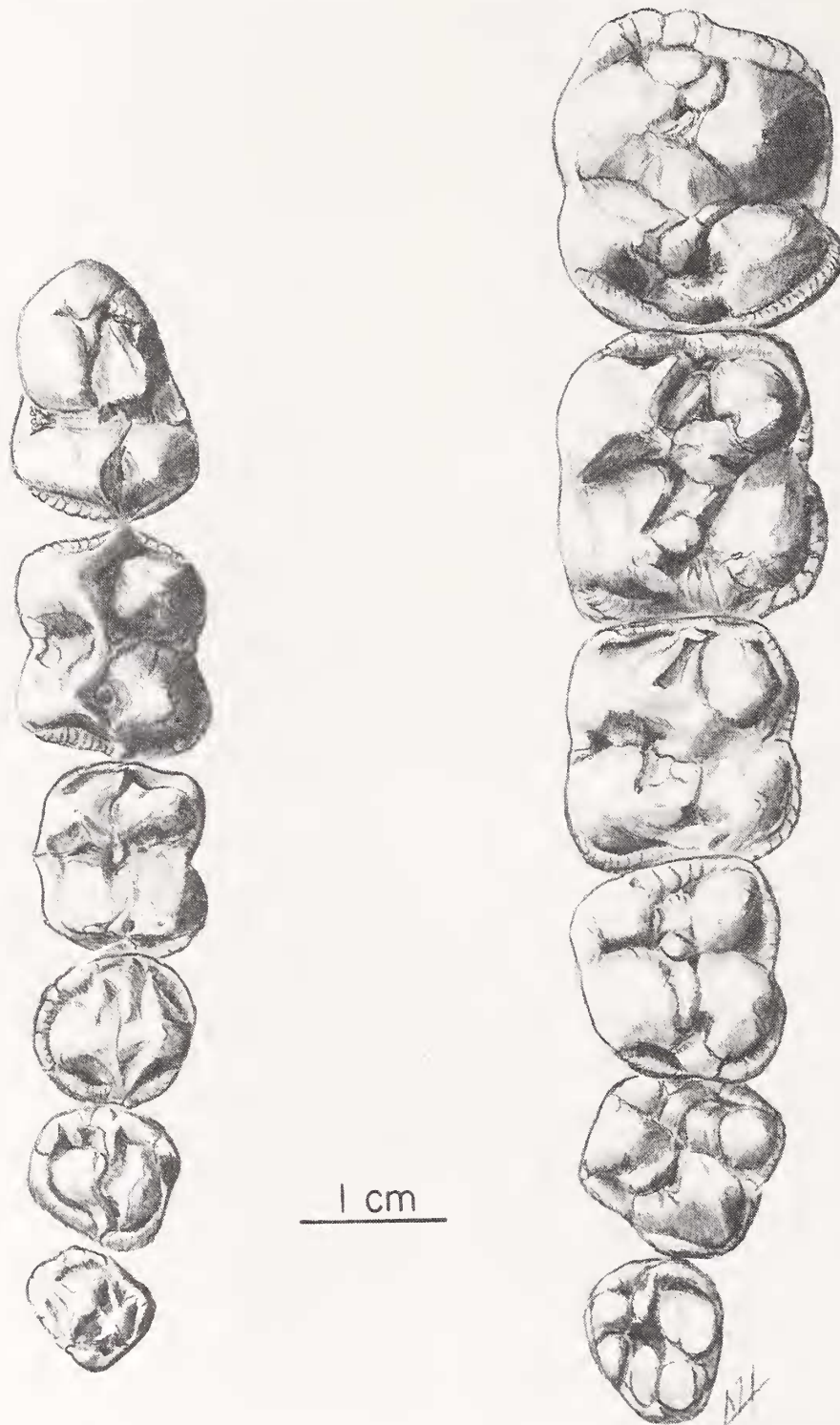
1 cm

Fig. 3. Right maxillary toothrows, P²-M³. Left, *Platygonus compressus*, CM 20114, Welsh Cave, Kentucky. Right, *Catagonus wagneri*, CONN 16886, Chaco of Paraguay. Artist, Mary M. Hubbard.
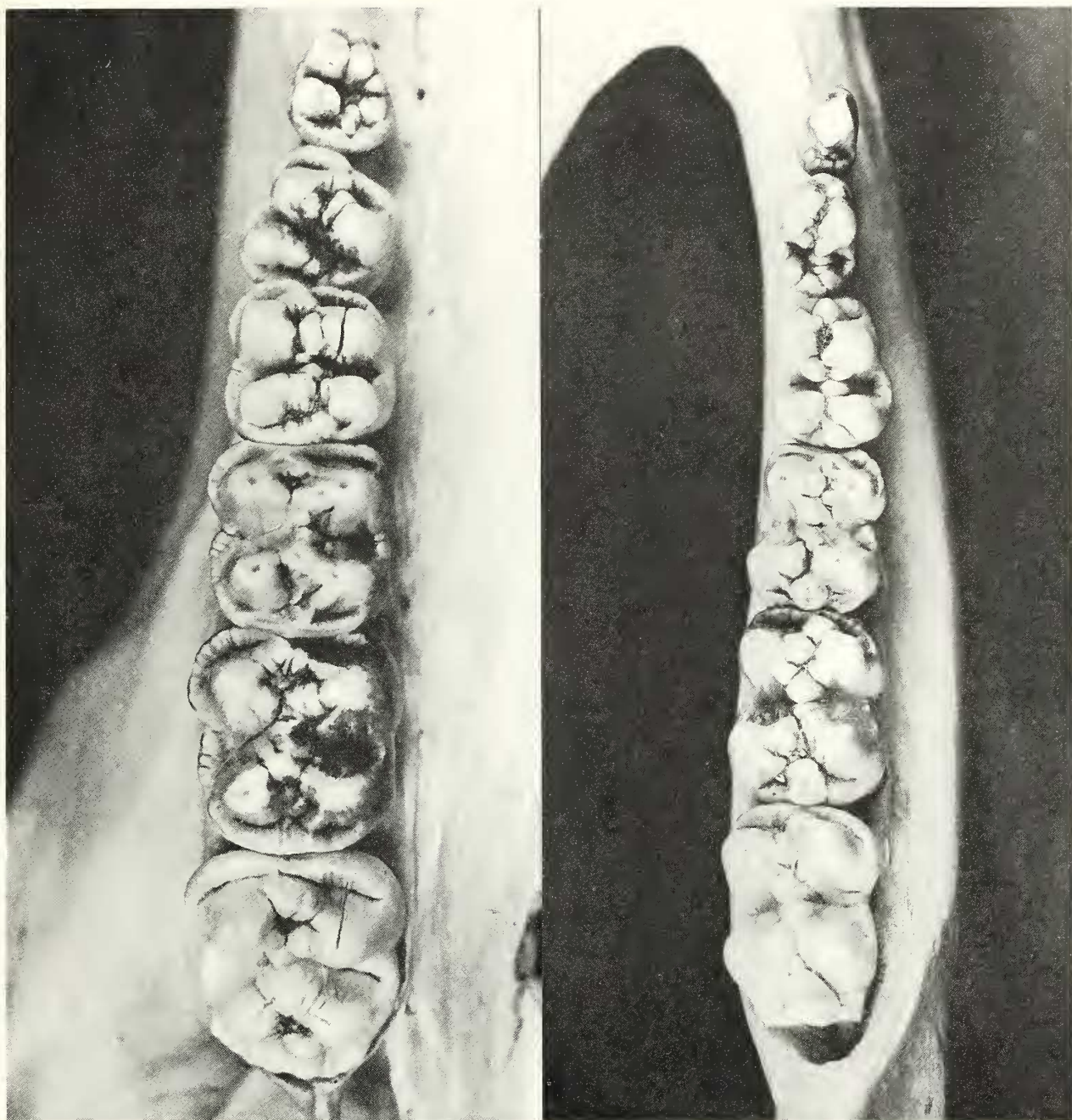
Fig. 4. Right cheek teeth, *C. wagneri*, CONN 16886. Left, maxillary P^2-M^3. Right, mandibular P_2-M_3.

Table 3. Anteroposterior and transverse diameters of M^2 and M^3 for *Brasiliochoerus* and *Catagonus*. Except where stated otherwise, measurements are from Rusconi (1930).

	M^2	M^3
Platygonus (Brasiliochoerus) platensis	16.3/15.5	15.5/13.5
P. (Brasiliochoerus) platensis parodii	17.3/16	16 /14.3
P. (Brasiliochoerus) stenocephalus, Reinhardt (1880:295)	18 /18	17 /16
P. (Brasiliochoerus) stenocephalus?*, Ameghino (1889:575)	16 /16	16 /13
Catagonus bonaerensis	19.6/18	22 /18
C. carlesi	19.8/18.5	22 /20
C. wagneri, Ȳ, holotype and paratype, Rusconi (1948:235)	19.6/19.5	21.5/19.5
C. wagneri, Recent of Paraguay, this study	20.6/18.8	22.3/18.9

*Considered by Rusconi (1930:176, 219) to be "*Catagonus (Interchoerus)*?"

orbital foramen near the middle of the rostrum occur in *Catagonus, Mylohyus, Prosthennops, Brasiliochoerus,* and most of the remaining species of *Platygonus.* These two charaters are in contrast to *Tayassu* where the glenoid fossa is posterior to the orbit and the infraorbital foramen lies in the posterior third of the rostrum. Partial exceptions, discussed later, occur in those South American *Platygonus* that also display other features suggesting some proximity to the ancestry of *Tayassu.* (3) Slender, gracile skulls occur in *Catagonus, Brasiliochoerus,* and some early *Platygonus* as opposed to the more massive skulls with flaring zygomata and angular processes and large canine buttresses of most *Platygonus* and *Prosthennops.* (4) Long toothrows and short diastemas occur in both *Catagonus* and *Brasiliochoerus.* The general similarity of *Catagonus* and *Brasiliochoerus* may be seen by comparing *C. carlesi* in Rusconi (1930: Plates 3, 4, 5) for the former genus with *P. stenocephalus* in Reinhardt (1880: Plate 7) and Winge (1906: Plate 6) for the latter subgenus. Only the M^2 vs. M^3 differences noted above and the larger premolars and molars of *C. carlesi* appear to separate the two taxa. If *Platygonus* is restricted by non-molariform premolars, *Brasiliochoerus* must be removed from the genus as Woodburne (1968:32) believed should be done eventually. The question then remaining would be the use of *Brasiliochoerus* as a genus, or as a subgenus of *Catagonus,* a question that cannot be resolved here.

Catagonus wagneri (Rusconi)

Platygonus carlesi wagneri Rusconi, 1930:231.
Platygonus wagneri.—Rusconi, 1948:231.
Catagonus wagneri.—Wetzel, Dubos, Martin, and Myers, 1975:379; Wetzel and Crespo, 1976:25.

TYPE-LOCALITY: Pre-Hispanic deposits, Argentina, Santiago del Estero, Llajta Mauca, 28°12′S, 63°05′W (Fig. 2).

RECENT RANGE AND HABITAT: Semiarid thorn-forest and steppe of the Gran Chaco; specimens reported in this study (Fig. 2) are from the middle to western Chaco of Paraguay and the province of Salta, Argentina. Interviews with hunters indicate that the present range extends into the Chaco of Bolivia and the Argentine provinces of Formosa, Chaco, and northern Santiago del Estero. Olrog, Ojeda, and Barquez (1976) report specimens from Nueva Esperanza, Depto. Pellegrini, in the latter province, as well as information on the tagua in the Chaco of Salta.

COMPARISONS

EXTERNAL APPEARANCE AND MEASUREMENTS: Compared with the gray color of *T. tajacu* and the black of *T. pecari, C. wagneri* is a large brownish-gray peccary with a faint collar of lighter hairs across the shoulders. Hair on ears and legs is longer and paler in color than in *Tayassu.* The head is larger, and ears, legs, and tail are longer. The larger ear accounts, no doubt, for one of the local names, Curé-buro. Like *T. pecari* and *T. tajacu, C. wagneri* has vestigial hooves or dew claws on the reduced second and fifth digits of the forefeet. A single, median dewclaw is present on the posterior side of the hindfeet of *T. pecari* and *T. tajacu* but absent in *C. wagneri.* Dew claws are missing altogether in the extinct *P. compressus* and *P. cumberlandensis* (Guilday et al., 1971:291).

Mean measurements of five freshly killed adults and one young adult *C. wagneri* from the vicinity of Teniente Ochoa and Tte. Enciso in the western Chaco of Paraguay are as follows: Length of head + body, 1026 (♂♂ 1112, 923; ♀♀ 1005, 1005, 1087); length of tail, 86.7 (♂ ..., 102; ♀♀ 88, 70, ...); length of hindfoot to tip of longest hoof, 227.6 (♂♂

222, 235; ♀ ♀ 228, 238, 215); height of ear from notch, 119.4 (♂ ♂ 115, 118; ♀ ♀ 120, 120, 124); weight, one ♀ , 37 kg.

Although most of our Paraguayan specimens of the three species of peccaries are skulls from hunters' kills, the external measurements of *C. wagneri* may be compared with the following means for five adult *T. pecari* (USNM), collected by the Smithsonian Venezuelan Project from the states of Apure and Bolívar, and two adult *T. tajacu* (CONN), from Sgto. Rodriguez, Depto. Nueva Asunción, Paraguay, respectively: Length of head + body, 1049.6 and 841; length of tail, 38.2 and 55.0; length of hind foot including hoof, 220 (N = 1) and 188; height of ear from notch, 82.0 and 92.0 One of the foregoing *T. pecari* weighed 26.9 kg. The greater size and weight of *C. wagneri* are obvious except for length of head + body. The overlap of this measurement with that of *T. pecari* reflects the relatively short postcranial dimensions of *C. wagneri*. The greater size of the Taguá's head is responsible for the saying among hunters in the Chaco that when the head is cut off, one is left with only half the animal. Larger cranial size in the Taguá is illustrated by comparing the greatest length of skulls of adult *C. wagneri* with those of *T. pecari*, all CONN specimens from Paraguay: 309.9 (O.R., 298-324; N = 29) and 271.7 (254-282; N = 20).

The ratio of distal to proximal elements of the limbs of *C. wagneri* is comparable to *Platygonus compressus* and *Mylohyus nasutus*, rather than to *Tayassu* (see Table 4). This type of comparison, made by Guilday et al. (1971:291), assumes that the ratio of length of scapula to humerus or the ratios of lengths

of the more distal limb elements to the humerus or femur are all greater in more cursorial mammals. Although limb bones in *C. wagneri* are shorter than in *C. compressus,* their measurements are generally nearer those of the latter species than of either *Tayassu.* Comparative mean lengths of metapodials of *C. wagneri* (Table 1) and *C. compressus* (Welsh Cave, Kentucky), respectively, follow: Metacarpal III, 67.4 and 85.5; metacarpal IV, 69.8 and 86.3; metatarsal, 82.4 (IV) and 91.1 In *C. wagneri,* metatarsals II and V are vestigial; phalanges and hooves for these digits are lacking. In *Platygonus,* metatarsal II is vestigial and V is lacking; in *Tayassu,* II is complete and V is vestigial (Guilday et al., 1971:291). As in *Tayassu,* digits II and V of the forefoot of *C. wagneri* are complete with hooves, phalanges, and articular surfaces on the distal ends of metacarpals. In addition to the evidence of limb proportions, the digits of *C. wagneri* suggest a species that is more cursorial than *Tayassu* but less cursorial than *Platygonus.*
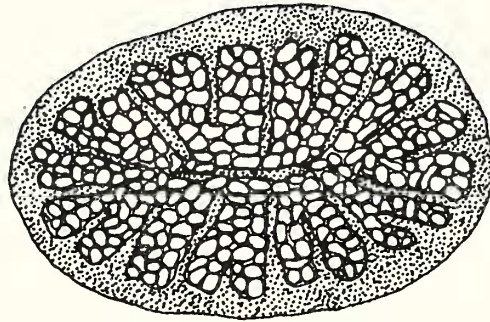
HAIR: The dorsal hairs or bristles, reaching 220 mm, are longer than in other peccaries (Fig. 5). The basal third to half (65-100 mm) of the shaft, strikingly paler than the terminal portion, is indistinctly banded by alternate shades of grayish-tan and off-white. This pale portion gradually merges into a band of dark brown (15-20 mm), followed by a narrower band of white (8-13 mm), and then by a long (65-80 mm) apex of dark brown to black. The shorter, less numerous hairs range from entirely dark brown or black for the shortest (approximately 40 mm) hairs to those with a beginning of a banded pattern. Pronounced apical fraying results in a plumose termination in all but the shortest hairs. In *T. pecari,* hair has a much

Table 4. Relative scapula and limb proportions of selected Tayassuidae; measurements in parentheses. Data for *C. wagneri* (Ȳ CONN 17803 and 18006) are from this study and for all other species, from Guilday, Hamilton, and McCrady, 1971:291.

Skeletal element	*Tayassu tajacu*	*Tayassu pecari*	*Platygonus compressus*	*Mylohyus nasutus*	*Catagonus wagneri*
scapula / humerus	95%	90%	99%	——	99% (171.6/173.9)
radius / humerus	69% (95.6/138)	72% (119/166)	78% (160/206)	84% (182/217)	81% (140.6/173.9)
metacarpal IV / humerus	36% (49/138)	38% (63.3/166)	45% (92.1/206)	47% (103/217)	40% (70.2/173.9)
tibia / femur	94% (135/144)	94% (161/172)	99% (198/201)	105% (230/216)	101% (177.0/175.0)
metatarsal IV / femur	41% (59/144)	——	46% (92.4/201)	53% (115/216)	47% (82.6/175.0)

Fig. 5. Dorsal hair of peccaries; left, *C. wagneri;* middle, *T. tajacu;* right, *T. pecari.*
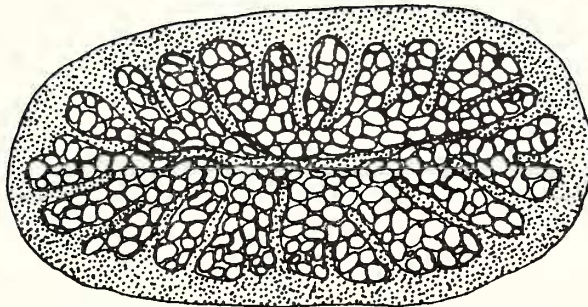
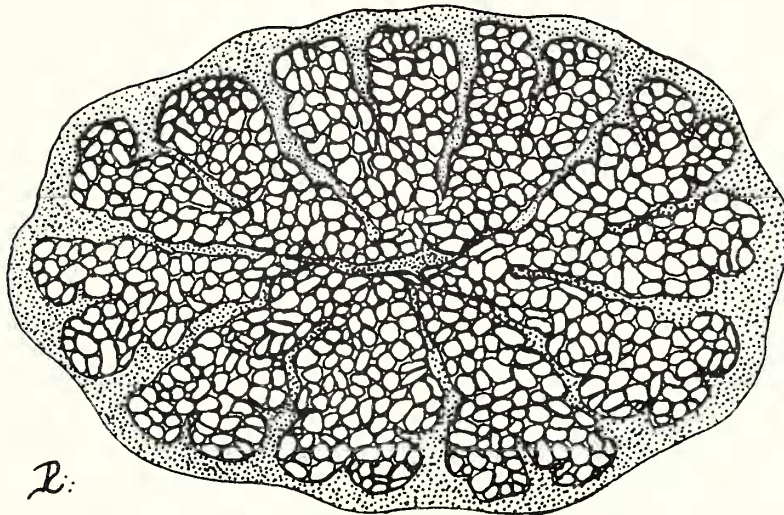Fig. 6. Hair of the peccaries; cross sections of dorsal hair at middle of shaft. Note the undulating surface and thinner cortical layer for *C. wagneri* as compared with the smaller diameter, smooth surface and thicker cortical layer for *T. tajacu* and *T. pecari.*

shorter pale basal area, followed by dark brown to black on the remaining three-quarters of the shaft. In *T. tajacu,* hair lacks the pale basal portion entirely, having instead, a series of distinct contrasting bands of alternating light and dark along the shaft before the terminal dark tip. Hair is also much shorter than that of *C. wagneri,* not exceeding 150 mm in all specimens examined from Paraguay. The shortest hairs of *T. tajacu* are white rather than black, as in *C. wagneri.*

Scanning electron micrographs indicate that in *C. wagneri* the hair surface has undulations or shallow grooves that are absent in both *Tayassu.* This feature can be seen better in cross sections prepared for light microscopes. Figure 6 illustrates these undulations, the larger diameter, and thinner cortical layer of *C. wagneri.* I measured diameter and minimal depth of the cortical layer, between the internal radial ribs, at the base, middle, and tip of hairs of the three peccaries. The thinness of the cortical layer in *C. wagneri* is illustrated by the means (in microns) and the ratio of minimal depth of the cortical layer to greatest diameter of the section as follows: *C. wagneri,* 17 (O.R., 15-20; N = 14) and .02 (.02-.03; N = 12); *T. pecari,* 37 (30-50; N = 20) and .06 (.05-.12; N = 10); *T. tajacu,* 28 (20-35; N = 11) and .06 (.05-.06; N = 9).

SEXUAL DIMORPHISM: Since most specimens of the Chacoan peccary are skulls from hunters' kills, sexes are chiefly unknown, but it is obvious that the variation of the canines and surrounding bone is not as extreme as in *P. compressus.* Coefficients of variation for *C. wagneri* and for *P. compressus* (Guilday et al., 1971: 293) are respectively: Width across upper canines, 2.86 and 10.65; width across canine buttresses, 3.03 and 12.26. When the sample of adult *C. wagneri* is divided by a combination of size of canines and width across canines, the group with the larger canines has a wider skull and somewhat shorter postcanine diastema and condylobasal length. The magnitude of variation is reduced by this segregation, a major reduction occurring in the zygomatic breadth from s = 10.8 for the unstratified group to s = 4.4 for the large-canine group, and 2.1 for the small-canine group. I am reluctant to associate size of canines with sexual dimorphism in *C. wagneri* because of the lack of clear-cut separation of "males" and "females." Since the more gracile skull of *C. wagneri* lacks the extreme development of canine buttresses and has less variation in canines, the possible effects of both age and any sexual differences are less accentuated than in *P. compressus.*

EXTERNAL NARES: Height of the nasal opening is greater in *Catagonus* than in *Tayassu,* as follows, with the mean, if given, followed by s: *Catagonus metropolitanus* 38; *C. carlesi* 28; *C. wagneri* 31.2, 1.2 (O.R. = 29.0-33.3; N = 23); *Tayassu pecari* 24.8, .80 (23.3-26.6; N = 18); *T. tajacu* 20.7, .71 (19.7-22.5; N = 18). In *Catagonus wagneri, C. carlesi, Platygonus compressus, P. cumberlandensis,* and *Tayassu pecari,* the most posterior lateral margin of the nares (= narial notch) is well posterior to I². In *T. tajacu* the narial notch is broader, not so deep, and falls above the posterior part of I². In *T. pecari* the narial notch differs from both *T. tajacu* and *C. wagneri* in being acuminate. *C. wagneri* differs from both *T. pecari* and *T. tajacu* in having a broadly curved midlateral projection, a process of the premaxilla, which divides the narial notch into subequal dorsal and ventral arcs. Where a slight projection occurs in the narial notch of *T. pecari* and *T. tajacu* from Paraguay, the projection is formed by the nasal bone rather than the premaxilla.

ROSTRUM: The much greater size of the rostrum, in both actual measurement and in proportion to the postrostral length of skull, separates *Catagonus* and *Platygonus* from the shorter-nosed members of *Tayassu.* Note in Table 5, however, that the postrostral to rostral ratios of *Platygonus* from the Lower Pleistocene of Argentina are approximately midway between *Tayassu* on one hand and *Platygonus* of North America and *Catagonus* on the other. The ratio of *Platygonus* sp. (MHN 305) is nearest to ratios of *Tayassu.*

The lateral profile of the rostrum in *Catagonus, Platygonus compressus,* and *P. cumberlandensis* is distinctly convex. The rostrum in *Tayassu pecari* is slightly concave in profile; in *T. tajacu, Platygonus scagliae, P. chapadmalensis* (MMCN 246), and *Platygonus* spp. (MHN 305, MMCN 1212), slightly convex or straight. In transverse section, the dorsum of the rostrum is broadly rounded in *Catagonus* and *Platygonus,* more sharply rounded in *T. tajacu,* and flat in *T. pecari.*

Woodburne (1968:28) used the well-defined anterior portion of the supraorbital canals in *T. tajacu* as a distinction between that species and *T. pecari.* In Paraguayan specimens of *C. wagneri* and *T. pecari,* the anterior portion of the canals varies from indistinct to, in the older specimens, as deep and well defined as the canals in *T. tajacu.* The anterior portions of the canals are also well defined in *Platygonus scagliae, P. chapadmalensis* (MMCN 246), *Platygonus*

Table 5. Comparison of ratios* of postrostral to rostral length and of position of infraorbital foramen to rostral length for *Catagonus,* *Platygonus,* and *Tayassu.* See text for explanation of abbreviations.

	PRL / RL adj.	Orbit to infraorbital foramen / RL
Catagonus wagneri, Recent	.37, s .02, N 15	.47, s .02, N 14
Catagonus sp., MMCN 41, Mid-Pleist., Argentina	.36	. . . .
Platygonus compressus, CM 12885, 12886, 20114, U-Pleist., N. Am.	.37 (. . . , .37, .38)	.44 (.46, .43, .44)
P. cumberlandensis, USNM 8000, 8146, 8147, Mid-Pleist., N. Am.	.36 (.38, . . . , .33)	.42 (.40, .43, . . .)
Platygonus sp., MMCN 1212, L-Pleist., Argentina	.48	.41
P. scagliae, MMCN 156, L-Pleist., Argentina	.48	.41
P. chapadmalensis, MMCN 246, L-Pleist., Argentina	.48	.31
Platygonus sp., MHN 305, Pleist., Brazil	.51	.30
Tayassu tajacu, Recent	.59, s .02, N 17	.30, s .02, N 19
T. pecari, Recent	.60, s .03, N 13	.23, s .01, N 17

*Measurements for *C. wagneri* are from Table 1. Pertinent measurements for other specimens follow. Measurements in parentheses are for individual specimens; $\bar{Y}$, s, and N are given for *T. tajacu* and *T. pecari.*

	PRL	RL adj.	Orbit to infra-orbital foramen	RL
Catagonus sp.	71	195	. . .	200
P. compressus	76 (. . . , 74, 77)	202 (. . . , 202, 202)	90.5 (93, 88, 90)	205.8 (203, 207, 207)
P. cumberlandensis	90 (97, . . . , 82)	251 (255, . . . , 246)	111 (103, 119, . . .)	261 (260, 275, 250)
Platygonus sp.	112	232	97	237
P. scagliae	92	178	72	184
P. chapadmalensis	91	190	61	194
Platygonus sp.	97	190	58	194
Tayassu tajacu	73.7, 4.7 N=17	124.8, 6.1 21	35.1, 2.9 19	127.5, 6.1 22
T. pecari	88.8, 3.7 N=13	150.2, 6.4 18	38.5, 3.5 19	153.0, 5.1 19

sp. (MMCN 1212), and in the lateral views of *P. stenocephalus* (Winge, 1906: Plate 6), and *Catagonus carlesi* (Rusconi, 1930: Plate 3). All these specimens from the Pleistocene were adults with evident molar wear. Thus the definite outline or sculpturing of the anterior canals, per se, is not a unique character of *T. tajacu* or *Dicotyles* vs. *Tayassu,* and especially not of older animals. The anterior canals of *T. tajacu,* being located nearer the summit of the dorsal rostral curve, are more evident from dorsal view. The anterior canals of *C. wagneri, P. compressus,* and *T. pecari* are located more laterally on the rostrum and are thus more broadly separated than the constricted anterior canals of *T. tajacu.* The anterior canals shown for *C. carlesi* by Rusconi (1930: Plates 3, 4) appear to be within the range of variation of *C. wagneri,* and

should not, in my view, be used as evidence of relationship of *C. carlesi* to *T. tajacu* as Woodburne (1968:32) suggested.

INFRAORBITAL FORAMEN (Table 5): In *C. wagneri* and *C. carlesi,* the anterior opening of this foramen is almost halfway between the orbit and the tip of the premaxilla, lying above P[4]. This position is approximated in *Platygonus* from North America and in some of the specimens from South America, such as *P. scagliae* and *Platygonus* sp. (MMCN 1212). The remaining specimens from South America, *P. chapadmalensis* (MMCN 246) and *Platygonus* sp. (MHN 305), are similar in this respect to *T. tajacu.* In both species of *Tayassu* the opening is in the posterior third of the rostrum, above P[4] or M[1]. In *T. tajacu* it lies under the anterior part of the zygomatic arch, and in

Table 6. Comparison of suborbital zygomatic depth in Recent peccaries from Paraguay, and specimens from the Pleistocene of Argentina, Brazil, and North America. See text for explanation of abbreviations.

	Suborbital zygomatic depth	Ratio of suborbital zygomatic depth / PRL
Platygonus cumberlandensis, USNM 8000, Mid-Pleistocene, North America	79.6	.82
Platygonus chapadmalensis, MMCN 246, Lower Pleistocene, Argentina	42.8	.47
Platygonus sp., MMCN 1212, Lower Pleistocene, Argentina	49.6	.44
Platygonus scagliae, MMCN 156, Lower Pleistocene, Argentina	39.1	.42
Platygonus sp., MHN 305, Pleistocene, Brazil	39.0	.40
Platygonus compressus, AMNH 42781 & TUC 5-1277, Upper Pleistocene, North America	35.0 (35.0, 35.0)	.44 (.44, .45)
Catagonus wagneri, Recent, Paraguay	30.3, s 2.3, N 30	.43, s .04, N 15
Catagonus sp., MMCN 41, Mid-Pleistocene, Argentina	25.7	.36
Tayassu pecari, Recent, Paraguay	22.8, s 1.6, N 21	.26, s .02, N 13
Tayassu tajacu, Recent, Paraguay	17.5, s 3.9, N 22	.24, s .05, N 17

T. pecari, even more posteriorly, well under the zygomatic shelf. The transverse shape of the opening differs in all three Recent species. In *C. wagneri* the opening is ovoid and oriented vertically along its longest axis; in *T. tajacu,* the longest axis of the oval is directed dorsolaterally; in *T. pecari* the opening is narrow and slit-like.

ZYGOMA: In both *Tayassu pecari* and *T. tajacu,* the ventrolateral face of the maxillary zygomatic process is deeply excavated as the fossa for the *dilator naris lateralis* muscle (as described for *T. tajacu* by Woodburne, 1968) and the fossa extends anteriorly above the opening of the infraorbital foramen. *Catagonus wagneri, C. carlesi,* and *Platygonus compressus* differ markedly from *Tayassu* in having only a shallow, short fossa not extending anteriorly beyond the infraorbital foramen.

Vertical depth of the suborbital zygoma is much greater in *Catagonus* and *Platygonus* than in *Tayassu*. This is shown, both as ratios and as measurements, in Table 6. Depth of the suborbital zygoma is, however, less in the more gracile skull of *Catagonus* than in *Platygonus*. In *C. wagneri* and *Catagonus* sp. (MMCN 41), the suborbital zygoma lacks the distinct concavity on the lateral face found in *Platygonus*.

ORBITS: In *Catagonus* and *Platygonus,* the orbits lie posteriorly in the skull; the anterior margin of the orbit is distinctly posterior to the last molar; and the postorbital process of the zygomatic is dorsal to the glenoid fossa. In both *Tayassu,* the anterior margin of the orbit lies above either the M^2 or M^3 and the postorbital process of the zygomatic is well anterior to the preglenoid process. In *Catagonus* and *Platygonus* the eyes are thus set posteriorly behind a much longer rostrum, while in both *Tayassu,* eyes are more anteriorly positioned behind a shorter rostrum. A mid-horizontal line through the orbits of either *Tayassu* is dorsal to the anterodorsal tip of the rostrum.

In the genera *Catagonus* and *Platygonus,* compensatory shift in the orbital position took several evolutionary pathways that probably reduced interference of the longer rostrum with vision: (1) The entire frontal region, including the orbits, shifted dorsally well above the dorsal margin of the rostrum, as in *Platygonus scagliae, P. chapadmalensis* (MMCN 246), and *Platygonus* sp. (MMCN 1212). (2) Only the orbits became positioned more dorsally, nearer the upper margin of the skull, as in *Platygonus cumberlandensis* and *P. compressus,* as pointed out by Guilday et al. (1971:298). (3) The long axis of the orbits came to lie at a more oblique angle to the long axis of the skull, as in *Catagonus* and *Platygonus* except for *P. scagliae* and relatives, above. This position of the eyes, along with the basicranial flexure of the

Table 7. Comparison of cranial capacities of Recent peccaries, *Catagonus wagneri, Tayassu pecari*, and *T. tajacu*. All specimens are adults from Paraguay. See text for definitions of abbreviations.

Species	$\overline{Y}$	s	C	O.R.	N
Cranial capacity, ml.					
C. wagneri	114.1	7.9	6.9	102-130	22
T. pecari	158.9	5.1	3.2	150-167	9
T. tajacu	95.9	6.2	6.5	84-105	10
Cranial capacity / Condylobasal length					
C. wagneri	.42	.03	6.6	.37-.51	21
T. pecari	.67	.03	3.8	.62-.70	9
T. tajacu	.50	.04	7.5	.43-.53	8

skull discussed next, would permit forward vision when the head flexed in a feeding position, permitting less interference by the rostrum (see Guilday et al., 1971:304). (4) The eyes shifted to a more lateral position, e.g., as Guilday et al. (ibid:298) found for *Platygonus.*

SIZE OF BRAIN CASE: Measurements of cranial capacity (Table 7) indicate a proportionally much smaller brain than in *Tayassu.* The smaller skull of *T. pecari* has a greater cranial capacity than *C. wagneri,* while the O.R. of the cranial capacity of the smallest species, *T. tajacu,* overlaps with that of the large *C. wagneri.* The markedly lower ratio of cranial capacity to condylobasal length in *C. wagneri* is similar to its low ratio of postrostral length to rostral length, adjusted (Table 5). Both ratios are expressions of the long rostrum and short postrostral dimension in *C. wagneri.* It will be noted in Tables 1 and 5 that the postrostral lengths of the crania of *Catagonus* and *P. compressus* are much shorter than that measurement in *T. pecari,* and that the ratios of PRL/RL adj. in *Catagonus* and *Platygonus* are significantly lower than those in *Tayassu.* It is therefore to be expected that when the cranial capacities are estimated for fossil *Platygonus* and *Catagonus,* they will prove to have had proportionally smaller brains than *Tayassu.* This would have conferred a distinct advantage upon *Tayassu,* although Guilday et al. (1971:309, 311) doubt that *Tayassu* and *Platygonus* could have been competitors in North America. It is difficult to imagine, however, that *Catagonus* and *Tayassu* were not competitors in the shifting ecotone between forest and forest-edge habitats in South America. In all but dusty, open habitats, the greater success of *Tayassu* must have been assured.

BASICRANIAL FLEXURE: Distinct basicranial flexure, absent in *T. pecari* and *T. tajacu,* is remarkable in *Catagonus wagneri, Catagonus* sp. (MMCN 41), *Platygonus scagliae, Platygonus* sp. (MMCN 1212), *P. cumberlandensis,* and *P. compressus.* In these species the basioccipital region is directed more anterodorsally, and the basisphenoid, with an even more dorsal tilt, approaches the vertical. In Recent *C. wagneri,* the ventral surface of the basisphenoid is 65°-75° from horizontal as defined by the premolar-molar toothrow, compared to approximately 20° in *Tayassu.* Guilday et al. (1971:304) associated this flexure and the oblique long axis of the orbits in *P. compressus* with evolutionary adaptation for life in more open habitats. Such modifications would permit a horizontal direction of the main axis of sight even when the head was flexed in a grazing attitude. This is a reasonable suggestion, especially when correlated with the extreme rostral development in *Platygonus* and *Catagonus,* which would require cranial flexure for reduced impairment of vision in both grazing and nongrazing attitudes.

SINUSES: Extreme development of the sinuses, a distinctive feature of the skull of *Platygonus* (see Guilday et al., 1971), occurs also in *C. wagneri.* A pair of prominent suborbital sinuses project dorsolaterally to the pterygoid processes and posteriorly to the level of the tympanic bullae. Air passages connect the dorsal side of these sinuses with a posterior extension of the nasal chamber. The extreme posterior margin of the nasal chamber reaches the level, lateral to the midventral line, of the anterior part of the basisphenoid. The well-developed maxillary sinuses, the posterior extension of the frontal sinuses into the dorsal part of the parietal bones, the suborbital sinuses,

Table 8. Comparison of mandibles, *Catagonus*, *Platygonus*, and *Tayassu*. Where available, $\bar{Y}$, s, and N, or $\bar{Y}$ and N are given. Mandibular length is from condyle to anterior tip. Measurements of *P. compressus* are from Guilday et al. (1971:293).

Species	Length, mandible	Maximal height ramus	Depth at postcanine diastema	Depth at ant. margin M_1	Height, ramus L., mandible
C. wagneri, Recent, Paraguay	209.8, 5.7 N = 20	93.0, 3.5 20	23.4, 1.4 23	31.2, 1.8 23	.44, .02 19
Catagonus sp., MMCN 41, Mid-Pleist., Argentina	202	. . .	30.6	35.8	. . .
P. compressus, Welsh Cave, U-Pleist., Kentucky	218.1, 6.0 N = 12	94.6, 5.0 10	31.2, 1.5 18	39.0, 2.7 18	.43*
P. cumberlandensis, USNM 8147, 8921-3, Mid-Pleist., Maryland	278.3 N = 4	113 1	36.7 3	48.2 3	.41 1
Platygonus sp., MMCN 1212, L-Pleist., Argentina	270	. . .	40.9	50.1	. . .
P. chapadmalensis, MMCN 246, L-Pleist., Argentina	243	. . .	40.5	49.8	. . .
P. scagliae, MMCN 156, L-Pleist., Argentina	211	. . .	31.4	41.7	. . .
Tayassu pecari, Recent, Paraguay and northern Argentina	189.0, 4.3 N = 14	88.4, 3.3 14	29.2, 2.1 15	38.4, 2.9 15	.47, .02 13
T. tajacu, Recent, Paraguay and northern Argentina	152.4, 8.8 N = 19	72.6, 4.0 16	26.6, 1.4 18	32.2, 1.4 18	.47, .02 16

*ratio of $\bar{Y}$'s.

and the posterior extension of the nasal chamber result in the brain case of *C. wagneri* being nearly surrounded by air chambers. Finch, Whitmore, and Sims (1972:18) commented on the cul-de-sacs associated with the extreme development of sinuses in *Platygonus compressus:* "The passage of air through the nasal passage was thus very tortuous, which may have been an advantage in a dust-laden atmosphere." It should be added that such extreme development of the sinus-nasal system in *Catagonus* and *Platygonus* could serve as both a dust trap and a well-developed olfactory system, with the latter requiring the former in a dusty atmosphere. *Tayassu pecari* and *T. tajacu,* although sharing the familial development of sinuses about the dorsal and anteroventral part of the brain case, lack this extreme development of sinuses. The size of the cribiform plates, much smaller in *Tayassu,* also suggests a lesser dependence upon olfaction than in *Platygonus* and *Catagonus.*

MANDIBLE: As with the cranium, the mandible of *C. wagneri* is somewhat shorter than it is in the smallest *Platygonus,* and much longer than in the largest *Tayassu* (see Table 8). The body of the mandible is so slender that the depth is actually less than in the smallest peccary, *T. tajacu.* In both *Tayassu,* the

mandible is proportionally deeper and has a higher ratio of height of ramus to total length than in *Catagonus, P. compressus,* and *P. cumberlandensis.*

In *Tayassu,* the posterior margin of the mandible bulges distinctly beyond the condyles, but in *Catagonus* and *Platygonus,* it projects only slightly if at all. In the more massive skull of *Platygonus,* the angular process of the mandible flares laterally, in contrast to *Catagonus* and *Tayassu,* where the angular portion is deflected medially in a gentle curve, or is vertical. Like *Tayassu,* *C. wagneri* lacks the distinctive keel on the mandibular symphysis found in *P. cumberlandensis* and *P. compressus.* A slight keel is observable on the holotype of *P. scagliae* and on *P. chapadmalensis* (MMCN 246). Of the specimens of North American *Platygonus* examined, only those from the Upper Pliocene (Hemphillian) lacked a keel: Edson Quarry, Kansas (AMNH), Snake Creek Formation, Nebraska (AMNH), and Hagerman Formation, Idaho (USNM 13798). This keel and the lateral flare of the angular processes seem to be specialized features of the Middle to Upper Pleistocene radiation of *Platygonus* in North America, not occurring in the more gracile skulls of earlier *Platygonus* or the more conservative *Catagonus.*

SIZE OF TEETH AND DIASTEMAS: Despite the smaller

skull of *C. wagneri,* the teeth are larger than in many species of *Platygonus* and are proportionally larger than in any member of that genus. The maxillary toothrows of *C. wagneri* and *P. compressus* are compared in Figure 3. This longer toothrow is accommodated in the shorter jaw of *C. wagneri* through a reduction in length of diastemas. This is illustrated in Figure 7, where the maxillary postcanine diastema is plotted against the length of M$^{1-3}$. The premolars of *C. wagneri* are frequently at oblique angles to the main axis of the toothrow. I presume this is an effect of crowding caused by phylogenetic reduction of length of jaw not entirely compensated by reduction in diastemal space.
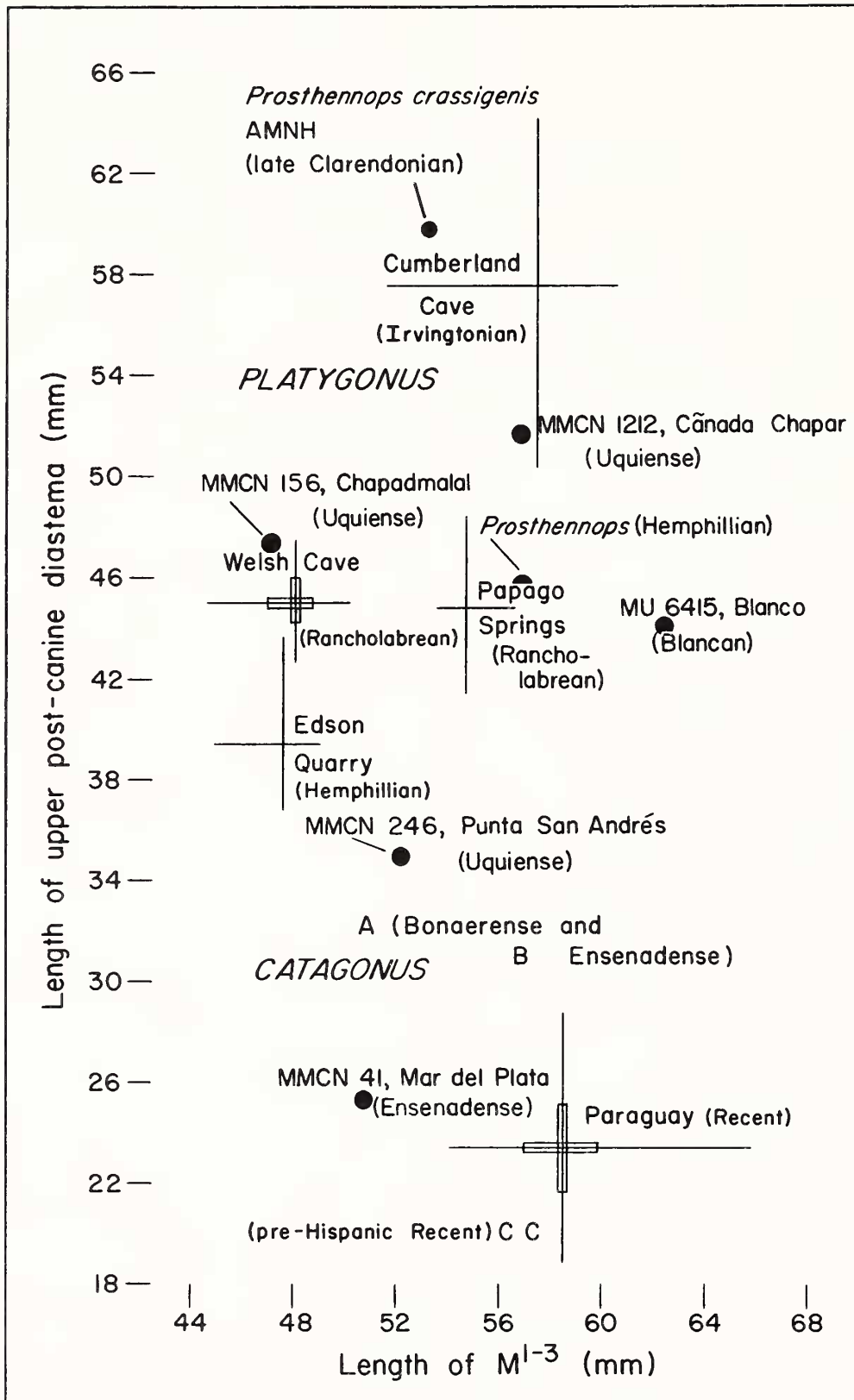
CUSPS AND CINGULA: The teeth of *Catagonus* are similar to *Platygonus* in being functionally lophodont and more hypsodont than in *Tayassu.* As shown in Figures 3 and 4, the premolars and molars of *C. wagneri* have numerous small cusps in addition to the major cusps that are characteristic of *Platygonus.* The cingula are well developed and surround the anterior, buccal, and posterior margins of P^2-M^3. Similar cuspules and well developed cingula occur in the holotype of *C. wagneri* (Rusconi, 1930: Plate 16) and on P^2-M^1 of *C. metropolitanus* (ibid.: Plates 8 and 9). Wear on the teeth of *C. carlesi* (ibid.: Plate 5) prevents inspection for cingula and cuspules. Although teeth of the holotype of *C. bonaerensis* are also worn, I was able to see pronounced cingula on the anterior faces of M^{2,3} and M$_{2,3}$ and cuspules at the boundaries between the anterior and posterior moieties of P$_4$ and M$_2$. In North American *Platygonus,* cingula on the buccal side of the molars are less well developed than in *Catagonus.* It should be noted, however, that in the temporal sequence of *Platygonus* examined, the buccal cingula of molars were more evident in the Blancan and Irvingtonian specimens than in the later Rancholabrean. Buccal cingula of the molars occur in the holotypes of *Platygonus marplatensis* and *P. scagliae,* in *P. chapadmalensis* (MMCN 246), and the large *Playtgonus* sp. (MMCN 1212). These specimens from the Upper Pliocene to Lower Pleistocene of Argentina, therefore, are intermediate in this character between *Catagonus* and North American *Platygonus.* In both *Catagonus* and *Platygonus,* cingula of the P$^{2-4}$ are well developed on the anterior and posterior faces and, for *Catagonus,* the buccal face and for *Platygonus,* the lingual face. In the mandible, no pronounced cingula occur on P$_{2-4}$ of *Catagonus* or *P. compressus,* but are well developed on the anterior, posterior, and buccal surfaces of P$_{3,4}$ of *P. cumber-*

landensis. Tayassu differs markedly from both *Catagonus* and *Platygonus* in lacking such well-developed cingula on premolars and molars. Where cingula do occur, they are restricted to portions of the anterior and posterior faces.

INCISORS: The incisors of *C. wagneri* are longer and the maxillary incisors more procumbent than are those of the other living peccaries. Across the posterior base of each incisor is a cingulum, absent in *T. pecari* and present on only the upper incisors of *T. tajacu.* A minute median cuspule, rather than a cingulum, is present on the unworn posterior face of the lower incisors of Paraguayan *Tayassu.* The unworn I^2 of *C. wagneri* differs from that of *Tayassu* in having a rounded tip, crenulated on its posterior margin, and a cavity in the occlusal (posterior) surface. A slight ridge partially divides the cavity into medial and lateral halves. The I^2 of *Tayassu* has a pointed tip without crenulations and without the cavity or median ridge on the posterior surface.

The size of the I^2, as measured transversely at the alveolus to avoid the effects of wear, does not differ greatly among *Catagonus, Tayassu,* and *Platygonus* from the Lower to Mid-Pleistocene of South America. However, I^2's in North American *Platygonus* from the Middle to Upper Pleistocene are smaller. The latter teeth are compared with *Catagonus,* with $\bar{Y}$ and s given where available: *C. wagneri,* 6.1 and .37 (O.R., 5.5-8.6; N = 15); *Catagonus* sp. (MMCN 41), 6.8; *P. cumberlandensis,* 5.2 (4.9, 5.5; N = 2); *P. alemanii,* Papago Springs, 5.5 (5.2-5.9; N = 4); *P. compressus,* Welsh Cave, 4.6 (3.3-5.6; N = 5). The statement of Guilday et al.. (1971:305) that the I^2 of *Platygonus* is ". . . reduced to a small peg . . ." reflects the small size of this tooth in some of the specimens from Welsh Cave.

As in *Tayassu,* all specimens of *C. wagneri* from Paraguay have three pairs of lower incisors, whereas I$_3$ is rarely present in North American Pleistocene *Platygonus.* One (CM 2634) of 15 undamaged mandibles of *P. compressus* from Welsh Cave has alveoli for I$_3$. One (AMNH 45719) of seven undamaged mandibles of the same species from Cherokee Cave, Missouri, has an alveolus for the left I$_3$. Of four complete mandibles of *P. cumberlandensis,* one (USNM 8147) has vestigial alveoli for I$_3$. The following intact mandibles of *Platygonus* from the North American Upper Pliocene have alveoli for I$_3$: One (USNM 13798) from the Hagerman Formation and six of seven specimens (AMNH) from Edson Quarry, Kansas. The small sample from the Pleistocene of Argen-

Prosthennops crassigenis
AMNH
(late Clarendonian)

Cumberland
Cave
(Irvingtonian)

PLATYGONUS

MMCN 1212, Cãnada Chapar
(Uquiense)

MMCN 156, Chapadmalal
(Uquiense)

Prosthennops (Hemphillian)

Welsh Cave

Papago
Springs
(Rancho-
labrean)

MU 6415, Blanco
(Blancan)

(Rancholabrean)

Edson
Quarry
(Hemphillian)

MMCN 246, Punta San Andrés
(Uquiense)

A (Bonaerense and
B   Ensenadense)

CATAGONUS

MMCN 41, Mar del Plata
(Ensenadense)

Paraguay (Recent)

(pre-Hispanic Recent) C C

Length of upper post-canine diastema (mm)

Length of M$^{1-3}$ (mm)

tina suggests a more conservative character: *Catagonus* sp. (MMCN 41) and *Platygonus* sp. (MMCN 1212) have I$_3$ on both right and left; *Catagonus* sp. (MMCN 707) and *P. scagliae* have I$_3$ or an alveolus present on only the right side; *P. chapadmalensis* (MMCN 246) has no alveolus for the right I$_3$ and probably none for the left.

CANINES: The canines of *Catagonus* and *Platygonus* are similar in being longer from alveolus to tip, and, in proportion to that length, more slender than the shorter, broader canines of *Tayassu*. The base of the canine in *C. wagnei* and *P. compressus* is smaller than in *T. pecari* and, as would be expected, in those peccaries with larger skulls such as *P. cumberlandensis* and *C. metropolitanus*. Anteroposterior and transverse diameters of the upper canine at its alveolus follow: *Platygonus alemanii*, Papago Springs, 14.2 and 10.4 (N = 4); *Catagonus wagneri*, Paraguay, 15.1 and 10.4 (N = 24 and 23); *C. wagneri*, holotype, 15.5 and 10; *C. carlesi*, holotype, 15.5 and 11; *C. metropolitanus*, 21 and 14; *P. cumberlandensis*, 20.0 and 14.3 (N = 3); *Tayassu pecari*, 16.3 and 11.0 (N = 9 and 10); and *T. tajacu*, 14.0 and 9.7 (N = 17).

P^2: The first upper premolar of *C. wagneri* is multicuspate and ovoid, with the anteroposterior diameter greater than the transverse. In *Platygonus*, the P^2 is bicuspate and has equal diameters; in *Tayassu*, the P^2 is roughly triangular in shape, its apex being an anterior lobe formed by the single large cusp. The anteroposterior diameter of *Catagonus'* P^2, although larger in proportion to its transverse diameter than in *Platygonus*, is approximately the same as in those *Platygonus* with large crania: *C. wagneri*, Paraguay, 11.4 (O.R., 10.1-12.8; N = 29); *Platygonus* sp. (MMCN 1212), 11.3; *P. cumberlandensis*, holotype and paratypes, 11.4 (N = 5); *P. texanus* (MU 6415), 10.9; *P. bicalcaratus* (TMM 31175-12), 11.3.

P$_2$: The first lower permanent premolar of *Catagonus* is proportionally narrow and has a single tall major cusp preceded by a low cuspule and followed by poste-

rior cuspules (Fig. 4). As in *Tayassu*, the P$_2$ lacks the laterally paired major cusps of *Platygonus*, but such cusps are present in the deciduous P$_2$ of *C. wagneri*.

P^3: The second upper premolar of *C. wagneri* has three major cusps, a variably larger number of cuspules, and definite cingula on the anterior, buccal, and posterior margins. It shares the character of three major cusps with *Tayassu*, and differs from *Platygonus* whose P^3 has two major cusps, transversely arranged, and a complete cingulum on the lingual instead of the buccal margin. Although the P^3 of *C. wagneri* is much larger than in *Tayassu*, *Prosthennops*, *Platygonus compressus*, *P. scagliae*, *P. chapadmalensis*, and *Platygonus* sp. of Edson Quarry, the O.R.'s of both diameters overlap with the diameters of *Platygonus* sp. (MMCN 1212), *P. cumberlandensis*, *P. texanus* (MU 6415), and *P. bicalcaratus* (TMM 31175-12). The P^3 of *Prosthennops* differs in being narrower; those of most *Platygonus* are wider than long; and those of *C. wagneri*, approximately equal in both diameters. This range is indicated by the following examples of ratios of transverse to anteroposterior diameter: *Prosthennops edensis*, .94; *Prosthennops* sp., Mixon Bone Beds, .92; *P. crassigenis*, .86 (N = 2); *Platygonus* sp. (MMCN 1212), 1.09; *P. chapadmalensis* (MMCN 246), 1.09; *P. compressus*, Welsh Cave, 1.11 (from Ȳ's of Guilday et al., 1971); *P. cumberlandensis*, 1.13 (O.R., 1.09-1.16; N = 5); *P. texanus* (MU 6415), 1.13; *Catagonus wagneri*, Paraguay, 1.00 (.88-1.11; N = 32).

P$_3$: Although similar to P$_2$, the second lower premolar of *C. wagneri* differs in being larger and in having the central, major cusp partially separated into lateral subdivisions. This is suggestive of the two transversely oriented cusps of *Platygonus* and *Tayassu*. The P$_3$ differs, like that of *Tayassu*, in lacking a cingulum, as contrasted with *Platygonus* in which a cingulum is continuous from the anterior and buccal to posterior face. Also like *Tayassu* but differing from *Platygonus*, the main cusp is preceded and followed by smaller cusps. The unworn anterior cusp of *C.*

Fig. 7. Comparison of Recent and fossil *Catagonus* with *Platygonus* and *Prosthennops*. A single line represents the observed range; a bar represents two standard errors of the mean of sample. Measurements are from this study and the literature, as follows: *Catagonus:* A, *C. carlesi*, holotype, Prov. Santiago del Estero (Rusconi 1930); B, composite, M$^{1-3}$ of *C. bonaerensis* and diastema of *C. metropolitanus*, Prov. Buenos Aires (ibid.); C, *C. wagneri*, holotype and paratype, Prov. Santiago del Estero (Rusconi 1948); MMCN 41, *Catagonus* sp., Prov. Buenos Aires; Paraguay, *C. wagneri*, Recent (N = 27 X and 31 Y). *Platygonus*, reading from top down: Cumberland Cave, Maryland, *P. cumberlandensis*, holotype and paratypes (N=4); MMCN 1212, *Platygonus* sp., Prov. Buenos Aires; MMCN 156, *P. scagliae*, holotype, Prov. Buenos Aires; Welsh Cave, Kentucky, *P. compressus* (Guilday et al. 1971); Papago Springs, Arizona, *P. alemanii* (N=3); MU 6415, *P. texanus*, Blanco Beds, Texas; Edson Quarry, Kansas, *Platygonus* sp. (N=3); MMCN 246, *P. chapadmalensis*, Prov. Buenos Aires. *Prosthennops:* *P. crassigenis*, Ainsworth area, Nebraska; *Prosthennops* sp., Mixon Bone Bed, Florida.
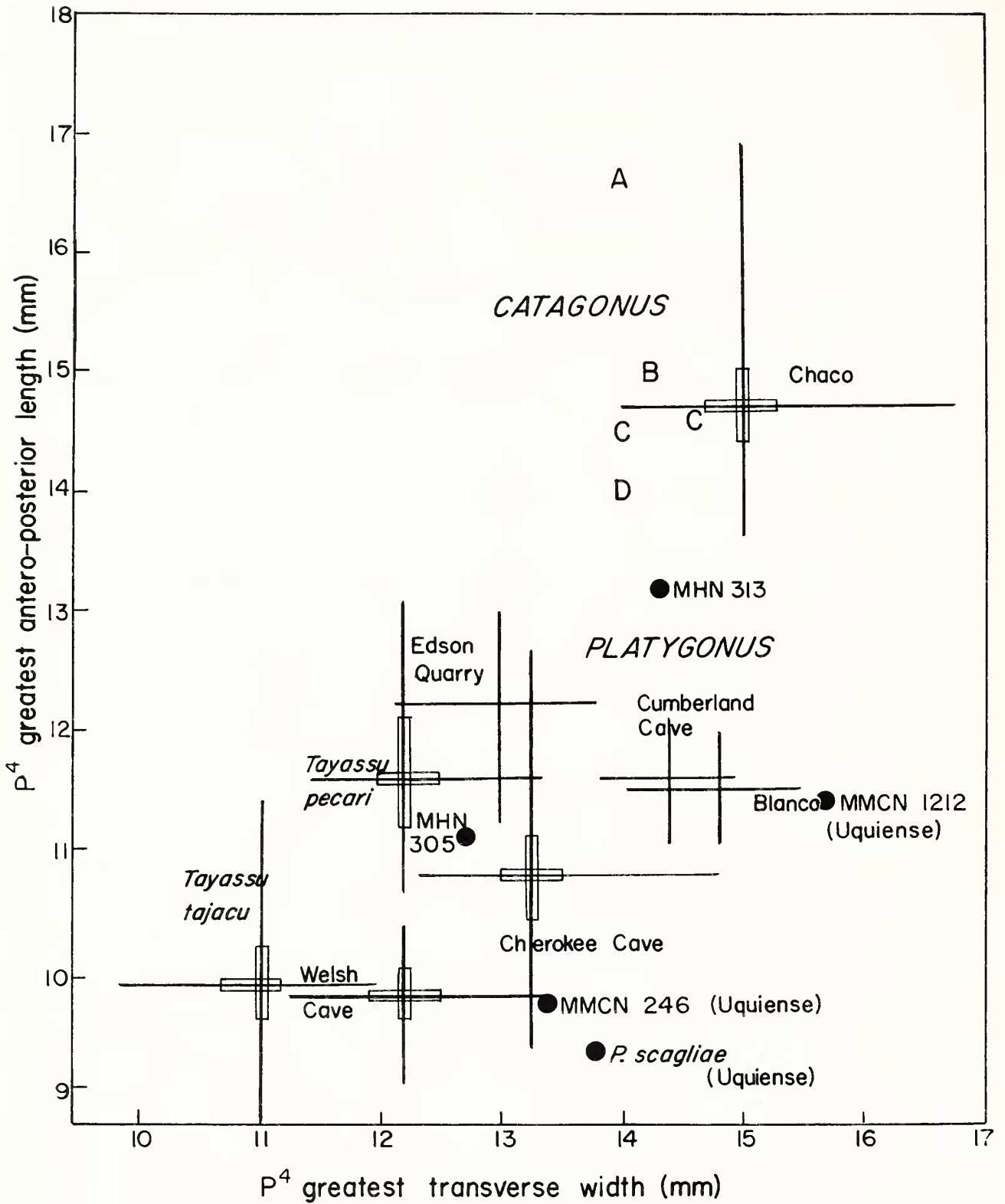
wagneri is crenulated, and the posterior mass consists of a series of at least three cuspules. In *Catagonus* both diameters of the P_3 are larger than those of *Tayassu*, most *Prosthennops, Platygonus* sp. of Edson Quarry, *P. compressus* of Welsh and Cherokee Caves, *P. scagliae,* and *P. chapadmalensis* (MMCN 246). A second group of *Platygonus* and allies with large crania, from the Upper Pliocene and Lower Pleistocene, have large, broad P_3's, with transverse diameters above the O.R.'s of *Catagonus,* while their anteroposterior diameters overlap the O.R.'s of the latter genus. The transverse diameters and, as it was used by Kraglievich (1959) to distinguish *Argyrohyus,* the ratios of transverse to anteroposterior diameters are contrasted between *Catagonus* and this second group: *Catagonus* sp. (MMCN 707), 8.9 and .63; *C. wagneri,* holotype, 9 and .66; *C. wagneri,* Paraguay, 8.8 (8.1-9.8; N = 19) and .69 (.62-.74; N = 24) vs. *Platygonus texanus,* 12.4 (11.3,13.5, Meade 1945) and .85 (.82, .89); *Argyrohyus chapadmalensis,* 10.7 and .88 (Kraglievich, 1959); *Platygonus marplatensis,* 10.2 and .85 (ibid.); *Platygonus* sp. (MMCN 1212), 10.05 and .82. These same ratios for the first group of *Platygonus* ranged from .77 (*Platygonus* from Edson Quarry) and .78 (*P. compressus* from Welsh Cave, from Ȳ's of Guilday et al., 1971) to .82 (*P. cumberlandensis* and *P. chapadmalensis*). The *Prosthennops* specimens (AMNH) differ by having very slender P_3 and low diameter ratios: *P. niobrarensis,* .62 (.60, .65) and *P. crassigenis,* .61.

P$_4^1$: The last permanent premolar of the genus *Catagonus* is molariform, nearly as large as the first molar, and has four major cusps. This is in contrast to *Platygonus,* which has much smaller P^4's with only two major cusps (Figs. 3 and 4). In Paraguayan *C. wagneri* (Fig. 8) the anteroposterior length of the P^4 (Ȳ, 15.0; N = 36) exceeds that of even the large *Platygonus,* MMCN 1212 (11.4) of the Lower Pleistocene of Argentina, as well as the large Blancan species reported by Meade (1945:528), *P. bicalcaratus*

(11.0, 11.4, 12.0) and *P. texanus* (14.0). Although in *Tayassu* and the *Prosthennops* examined, the P^4's are more molariform than in *Platygonus,* they do not have four equal major cusps nor do they attain anteroposterior diameter approaching that of the M^1. In *Tayassu,* the P^4 has only three major cusps. If the supernumerary teeth in the holotype of *P. (Brasiliochoerus) stenocephalus* (Winge, 1906: Plate 6) are molars, the P^4 apparently has four cusps and approaches the length of the molar.

The greater size of the P_4 of *Catagonus* as compared to *Platygonus* and relatives is illustrated by the following series of anteroposterior diameters: *C. wagneri,* Paraguay, 16.2 (14.4-19.4; N = 22); *Platygonus texanus* (MU 6415), 14.5; *Platygonus* sp. (MMCN 1212), 14.2; *P. bicalcaratus* (TMM 31175-12), 13.9; *P. marplatensis,* 13.0 (Reig, 1952:122); *Argyrohyus chapadmalensis,* 12.5 (Kraglievich, 1959:226); *Platygonus cumberlandensis,* 12.2 (N = 4); *P. chapadmalensis* (MMCN 246), 10.8; *P. compressus,* Welsh Cave, 10.8. Although all the foregoing specimens had smaller anteroposterior diameters than *Catagonus,* some of them had transverse diameters approaching that genus. The ratios of transverse to anteroposterior diameter reflect this character, as pointed out by Kraglievich (1959) for *Argyrohyus*: *Catagonus bonaerensis,* .78; *C. rebuffoi,* .72; *C. wagneri,* Paraguay, .77, s = .04 (.66-.82; N = 25) vs. *Platygonus marplatensis,* 1.00 (Kraglievich, 1959); *P. cumberlandensis,* .97 (.94-1.00; N = 4); *P. chapadmalensis* (MMCN 246), .95; *Argyrohyus chapadmalensis,* .93 (Kraglievich, 1959); *Platygonus texanus* (MU 6415), .92; *P. bicalcaratus* (TMM 31178-13), .91.

M^1: The anterior and posterior cingula are interrupted at mid-point by cuspules. A variable number of three to four cuspules lie between these anterior and posterior cuspules. As in the other maxillary cheek teeth, a cingulum on the buccal side is continuous with cingula of the anterior and posterior faces. Both diam-

◀ Fig. 8. Comparison of Recent and fossil peccaries; lines and bars as in Fig. 7. Measurements are from this study and from the literature as follows: *Catagonus:* A, *C. metropolitanus* and B, *C. bonaerensis,* holotypes, Prov. Buenos Aires, Mid-Pleistocene (Rusconi 1930); C, *C. wagneri,* holotype and topotype, Prov. Santiago del Estero, pre-Hispanic (Rusconi 1948); D, *C. carlesi,* holotype, Prov. Santiago del Estero, Mid-Pleistocene (Rusconi 1930); Chaco, *C. wagneri,* Paraguay, Recent (N=36). *Platygonus,* reading from top down: MHN 313, *Platygonus* sp., Caves of Minas Gerais, Pleistocene; Edson Quarry, Kansas, *Platygonus* sp., Upper Pliocene (N=5); Cumberland Cave, Maryland, *P. cumberlandensis,* holotype and paratypes, Mid-Pleistocene (N=5); Blanco Beds, Texas, *P. bicalcaratus,* Blancan (Meade 1945); MMCN 1212, *Platygonus* sp., Prov. Buenos Aires, Lower Pleistocene; MHN 305, *Platygonus* sp., Caves of Minas Gerais, Pleistocene; Cherokee Cave, Missouri, *P. compressus,* Upper Pleistocene (Simpson 1949); Welsh Cave, Kentucky, *P. compressus,* Upper Pleistocene (Guilday et al. 1971); MMCN 246, *P. chapadmalensis,* Prov. Buenos Aires, Lower Pleistocene; *P. scagliae,* holotype, MMCN 156, Prov. Buenos Aires, Lower Pleistocene. *Tayassu: T. pecari,* Paraguay, Recent (N=22); *T. tajacu,* Paraguay, Recent (N=18).

eters of the first upper molars of *Catagonus* are larger than those of *Tayassu, Platygonus compressus,* and *P. scagliae.* The transverse diameter of *Catagonus* is greater than that of *P. bicalcaratus* (MU 6415) and *P. chapadmalensis* (MMCN 246), but smaller than that of *P. texanus* (TMM 31175-12).

M_1: Cuspules occur near the midlines of the anterior and posterior cingula. Medial cuspules lie in the valley between the anterior and posterior pairs of major cusps. Unlike the M_1 of *Tayassu* and *Platygonus,* there is a definite cuspule on the lingual side of the valley between the two pairs of major cusps. In unworn M_1 this is flanked by a lesser cuspule in the buccal position. The anteroposterior diameter of the M_1 of *Catagonus* is larger than that of *Tayassu* or *Platygonus.* The transverse diameter overlaps that of *P. texanus* (MU 6415), *P. bicalcaratus* (TMM 31178-13), *P. cumberlandensis,* and *Platygonus* sp. (MMCN 1212).

M^2: Pronounced cuspules occur medially at the anterior and posterior borders of the second upper molar. As with the M^1, medial cuspules lie next to the valley between the two moieties. Cingula bind the buccal and, except for the interruption by cuspules, the anterior and posterior margins of the tooth. Both diameters of the M^2 of *C. wagneri* are larger than in *Tayassu, P. compressus, P. scagliae,* and *P. chapadmalensis* (MMCN 246). The O.R.'s overlap those of *P. texanus* (MU 6415), *P. bicalcaratus* (TMM 31175-12), *P. cumberlandensis,* and *Platygonus* sp. (MMCN 1212). The entire sample is dwarfed by the transverse diameters of *P. henningi* Rusconi (1930), 21.3; and *Catagonus* sp. (MMCN 707), 22.6.

M_2: The second lower molar is similar to M_1 except that it is larger in all dimensions and has more pronounced cuspules. In *Catagonus,* both diameters of this tooth are greater than those of *Tayassu, P. compressus, P. chapadmalensis* (MMCN 246), *P. scagliae,* and *Prosthennops.* The O.R.'s of both dimensions overlap those of *P. cumberlandensis, P. texanus* (MU 6415, 6416) and *P. bicalcaratus* (TMM 31178-13, 31197-2). Transverse diameter of the M_2 in the large *Platygonus* specimen (MMCN 1212) is 19.8, and that of *Catagonus* sp. (MMCN 707), 20.6 as compared to *C. wagneri,* $\bar{Y} = 16.5$ (O.R., 15.1-17.8; N = 27).

M^3: The last upper molar of *Catagonus* is quadrangular in outline, lacking the distinct posterior constriction in transverse width that occurs in *Tayassu, Mylohyus,* and most *Platygonus* and *Prosthennops.* Figures 3 and 4 show the four major cusps, the cuspules, and truncated appearance of the M^3. Some ratios of greatest transverse diameter of the posterior moiety to anterior moiety follow: *C. wagneri,* Paraguay, .92, s = .03 (O.R., .87-.96; N = 14); *Catagonus* sp. (MMCN 41), Mid-Pleistocene, Argentina, .96; *Platygonus bicalcaratus* (TMM 31175-12), Blancan, .89; *P. scagliae,* holotype, Lower Pleistocene, Argentina, .88; *P. compressus,* Upper Pleistocene, Missouri, .85 (Simpson 1949:29; ratio of means of W_p to W_a); *P. cumberlandensis,* Mid-Pleistocene, Maryland, .88 (.79-.96; N = 3); *Prosthennops crassigenis,* late Clarendonian, Nebraska, .86 (.81, .90); *P. edensis,* late Hemphillian, California, .93; *Prosthennops* sp., late Hemphillian, Florida, .86; *Tayassu tajacu,* Recent, Paraguay, .88 (.86-.95; N = 4); *T. pecari,* Recent, Paraguay, .88 (.82-.97; N = 9).

The appearance of posterior taper is accentuated in *Mylohyus, Tayassu,* and most *Platygonus* by the presence of a posterior lobe or heel as contrasted with the truncated M^3 of *Catagonus, Prosthennops,* and *Platygonus bicalcaratus.* The M^3's of *Catagonus* and *P. bicalcaratus* (TMM 31175-12)[1] are quite similar, both having a well-developed cingulum on the posterior margin The chief differences in *C. wagneri* are the less pronounced posterior taper and the presence of medial cuspules, including one dividing the posterior cingulum rather than the medial ridge that divides this cingulum in *P. bicalcaratus.*

Both diameters of the M^3 of *C. wagneri* are larger than those of *Tayassu, Platygonus compressus, P. scagliae, P. chapadmalensis, Platygonus* spp. (MHN 305, 313), and *Prosthennops crassigenis.* The O.R.'s

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[1] Hibbard and Riggs (1949, Bull. Geol. Soc. Amer., 60:829-860), followed by Dalquest (1975, Occ. Papers No. 30, The Museum, Texas Tech Univ.), considered *P. texanus* to be conspecific with *P. bicalcaratus.* It is convenient for discussion purposes here to retain the two species, following Meade (1945), rather than speak of "*texanus*-like *P. bicalcaratus*" with a distinct heel on the M^3 (MU 6415) and "typical *P. bicalcaratus*" with a truncated M^3 (TMM 31175-12).

Fig. 9. Canonical analyses, fossil and Recent peccaries, 21 variables as follows: condylobasal length, rostral length, greatest width ▶ across maxillary toothrow, palatal widths inside P^2's and M^2's, height of cranium at condyles, length of postcanine diastema, length of P^2-M^3, length of P^{2-4}, length of M^{1-3}, and anteroposterior and transverse diameters of individual maxillary teeth from P^3 to M^3. Except for *P. compressus,* Welsh Cave (Guilday et al. 1971), measurements are from this study. Note: *Platygonus* sp., MMCN 246=*P. chapadmalensis.*
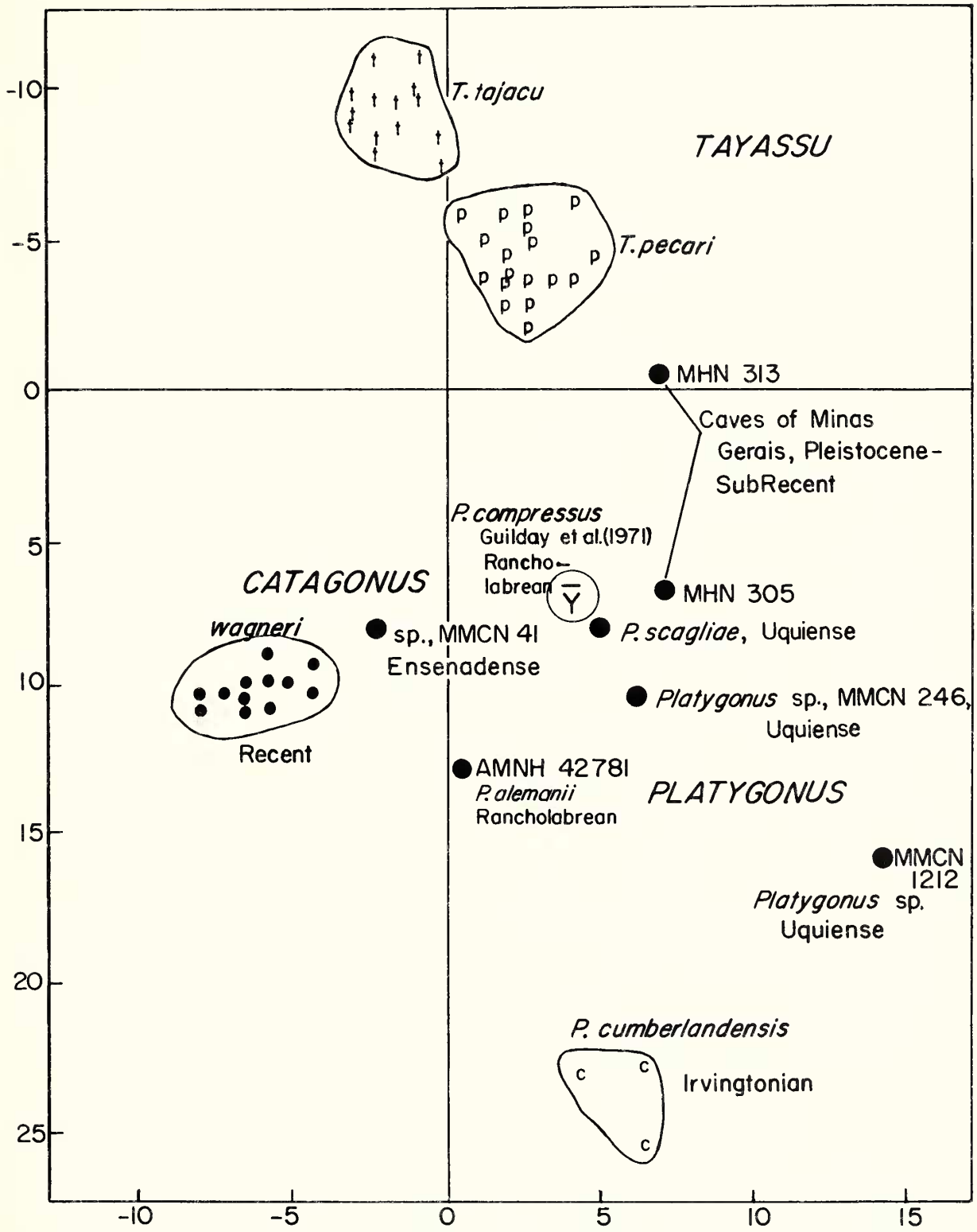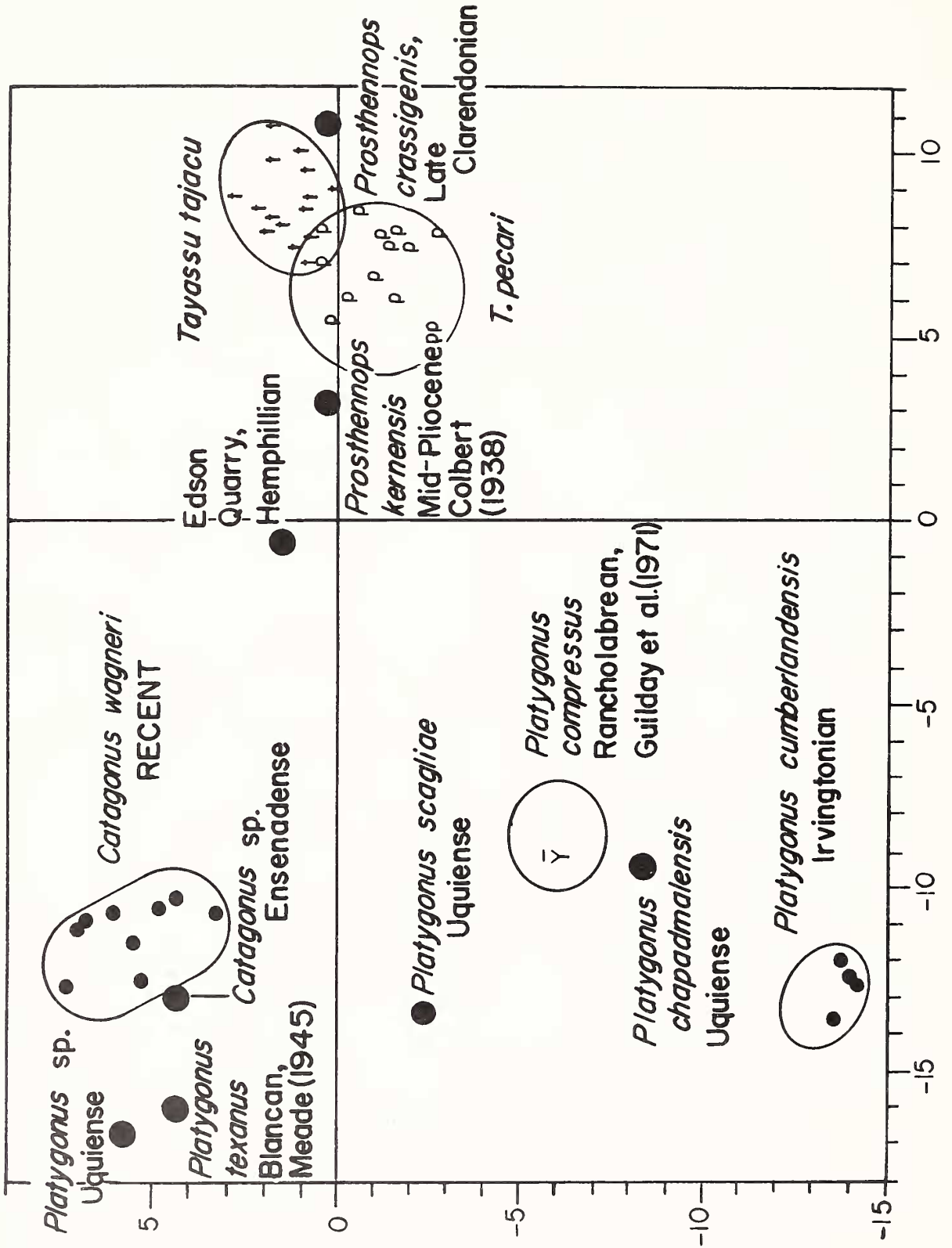
of the anteroposterior diameter overlap that of *Prosthennops edensis, Prosthennops* sp. from Mixon Bone Beds *Platygonus* spp. (MMCN 1212, MHN 309), *P. bicalcaratus,* and *P. marplatensis.* The M^3 of *C. wagneri* is much smaller in both dimensions than *Catagonus* sp. (MMCN 707), in transverse diameter than *P. bicalcaratus* and *P. marplatensis,* and in anteroposterior diameter than *P. texanus* (MU 6415).

M_3: The last lower molar differs from the truncated upper molar in having a large, median posterior cusp. This cusp (hypoconulid) in *Catagonus,* as well as in *Platygonus,* has an undivided point and is a prominent feature of the M_3, secondary in height only to the pair of major cusps in each moiety. The equivalent posterior lobe in *Tayassu* is highly variable, with numerous cuspules. In *Catagonus,* a cuspule lies on the buccal flank of the posterior cusp. The cingulum on the anterior face of the M_3 is interrupted by a median cuspule and the overlapping posterior cuspule of the M_2. A chain of medial cuspules extends from the

valley between the anterior pair of major cusps to the large posterior cusp.

The transverse diameters of the posterior and anterior moieties of M_3 in *C. wagneri* are nearly equal (Fig. 4), as compared with proportionally lesser widths of the posterior moiety in other specimens examined. This greater posterior taper is illustrated by the following ratios of transverse diameter of posterior moiety to anterior moiety: *C. wagneri,* Recent, Paraguay, .98 (O.R., .95-1.0; N = 10); *Platygonus compressus,* Rancholabrean, Missouri, .96 (Simpson, 1949:30; ratio of means of W_p to W_a); *P. cumberlandensis,* Irvingtonian, Maryland, .86; *P. bicalcaratus,* Blancan, .91 (N = 2); *P. texanus,* Blancan, .90; *P. marplatensis,* holotype, .89; *Prosthennops* sp., late Hemphillian, Florida, .90; *P. crassigenis,* late Clarendonian, Nebraska, .86; *P. niobrarensis,* Valentinian, Nebraska, .79; *Tayassu pecari,* Recent, Paraguay, .89 (.84-.94; N = 10); *T. tajacu,* Recent, Paraguay, .91 (.84-.97; N = 10).

DISCUSSION AND CONCLUSIONS

The close relationship of the genera *Catagonus* and *Platygonus* indicated in the foregoing comparisons is also supported by canonical analyses. Multivariant comparisons were made using width and length of mandibular teeth plus length of mandibular diastemas, maxillary teeth measurements, and all the measurements or combinations listed for Figures 9 and 10. In Figure 9, the specimens of *Catagonus* are positioned adjacent to the middle of the grouping of *Platygonus* specimens from the Pleistocene of both South and North America. This is also shown in Figure 10, except that the closeness of two large specimens of *Platygonus* to *Catagonus* is exaggerated. Some of the large dimensions of the teeth of *Platygonus* sp. (MMCN 1212) and *P. texanus* are similar to those of *Catagonus,* but when cranial dimensions are included in the multivariant comparisons, as in Figure 9, this relationship is not so close. Note also that in Figure 8 the dimensions of a single critical tooth, P^4,

of the Blancan specimens and MMCN 1212, are similar to each other and group with the rest of *Platygonus,* well separated from *Catagonus.*

The specimens of *Platygonus* from the South American Pleistocene, although separable from *Catagonus* by both multivariant and univariant comparisons, show some blending of *Platygonus* and *Catagonus* characters not noted in the North American *Platygonus. P. scagliae, P. chapadmalensis,* and *Platygonus* sp. (MMCN 1212), all from the Lower Pleistocene (Uquiense), have typical *Platygonus* P^4 (see Fig. 8), but show some similarity to *Catagonus* in cingula on the anterior and buccal sides of P^{2-4} and $M^{2,3}$. In the relationship of the maxillary postcanine diastema to length of M^{1-3}, *P. chapadmalensis* is also intermediate between *Catagonus* and *Platygonus* (see Fig. 7).

All multivariant comparisons, including those shown in Figures 9 and 10, positioned *Tayassu pecari* closely with *T. tajacu. Tayassu* is widely separated

◄ Fig. 10. Canonical analyses, fossil and Recent peccaries, 26 variables as follows: lengths P^2_2-M^3_3, P_{2-4}, M_{1-3}, anteroposterior and transverse diameters of individual teeth from P^3 to M^3 and P_2 to M_3. Measurements from the literature are indicated in figure; measurements from this study are as follows: *Catagonus: C. wagneri,* Paraguay, Recent; *Catagonus* sp., MMCN 41, Prov. Buenos Aires, Mid-Pleistocene. *Platygonus,* reading from top down: *Platygonus* sp., MMCN 1212, Prov. Buenos Aires, Lower Pleistocene; *Platygonus* sp., Edson Quarry, Kansas, Upper Pliocene; *P. scagliae,* holotype, MMCN 156, Prov. Buenos Aires, Lower Pleistocene; *P. chapadmalensis,* MMCN 246, Prov. Buenos Aires, Lower Pleistocene; *P. cumberlandensis,* holotype and paratypes, Cumberland Cave, Maryland, Mid-Pleistocene. *Prosthennops: P. crassigenis,* Ash Hollow Formation, Florida, Lower Pliocene. *Tayassu: T. pecari* and *T. tajacu,* Paraguay, Recent.

from *Catagonus* in all these comparisons, but near some *Prosthennops* (Fig. 10) and two *Platygonus*, MHN 313 (Fig. 9) and MHN 305 (Table 5). The latter specimens are from caves in the region of Lagoa Santa, Minas Gerais. These and other MNH specimens strongly suggest a phylogenetic continuum from *Prosthennops-Platygonus* to modern *Tayassu pecari*. As none of the Lagoa Santa specimens at MHN have M^2's larger than M^3's, as does *Platygonus (Brasiliochoerus) stenocephalus* (see Table 3), I have not followed Paula Couto's (1970:7) application of that name to the large specimens in that collection.

Woodburne (1968:30-32) hypothesized that a common ancestor of *T. pecari, P. (Brasiliochoerus) stenocephalus,* and *Mylohyus* would be *Prosthennops niobrarensis* Colbert (Valentinian, Lower Pliocene of Nebraska). The additional specimens from Minas Gerais at MHN, not seen by Woodburne, suggest that *T. pecari* originated in South America, probably either in the forested highlands of Brazil or during a period of isolation in a forest center in the Amazonian basin. Woodburne also believed there was an affinity of *T. tajacu* with the *Platygonus compressus* group and considered the similarity of their common ancestry to certain peccaries in the Frick Collection (AMNH)—the specimens from Edson Quarry, Kansas (Woodburne, pers. commun.). In the present study some comparisons place these Edson Quarry specimens in the genus *Platygonus*. In other comparisons they fall in an intermediate position with *Platygonus, Catagonus*, and *Tayassu,* and seem to support Woodburne's idea, but with *T. pecari* and *T. tajacu* more closely related to each other than to any other species. It is probable that *T. tajacu* evolved in South America from a proto-*T. pecari*. Both the more northerly extension of the range of *T. tajacu* and its much smaller size, which would have made available to them many more suitable dens in which the species could take refuge, suggest that the selective force was cold stress upon a population isolated in montane forests. In tracing origins of *T. pecari* separate from *T. tajacu,* Woodburne placed chief emphasis upon difference in origin of two muscles of mastication, but ignored the many common characters in which they differ from other genera. I would not challenge his excellent list of salient differences (ibid.:28-29), except for the minor note that exceptions to his differences, numbers 9, 19, 22, 26, and 27, have been encountered in peccaries from Venezuela and Paraguay. And, of course, I would use his list of characters as specific rather than generic differences.

The early history of *Catagonus* cannot be traced with the data at hand, but its close relationship to *Platygonus* seems apparent. In many respects, *C. wagneri* is more conservative than *P. cumberlandensis* and *P. compressus* of the Middle to Upper Pleistocene —in retention of dewclaws on the forefeet and the third pair of lower incisors, in failure to develop the flaring zygomata, angular processes and orbits, the canine buttresses, and the symphyseal keel. In these features and in the more gracile skull, *C. wagneri* more nearly resembles *Platygonus* of the Upper Pliocene. Also, the molariform premolars of *C. wagneri* are somewhat like those of *Prosthennops* of the Pliocene.

The more primitive features of *C. wagneri* suggest that its ancestry was not subjected to as severe selection toward a specialized cursorial existence in open habitats as has been suggested for *Platygonus* by Guilday et al. (1971). North American *Platygonus* was preyed upon by large, cursorial carnivores that were absent in South American grasslands. This may have provided a selective force developing a more cursorial group in North America (Guilday, pers. commun.). Another effect of greater predation pressure upon North American *Platygonus* might have been the selection of males with larger canines for defense of the herd. *Catagonus,* not subjected to this degree of selective predator pressure upon defenders of the herd, would retain a more ancestral, minimal sexual dimorphism. In support of this thesis, the variation in size of canines and canine buttresses in *Platygonus* is greater by five-fold than in *C. wagneri.*

Despite its more conservative evolution, *C. wagneri* retains those features of *Platygonus* that are probably adaptive for a cursorial life in an open, arid habitat: Greater size than the other modern peccaries, elongated limbs, basicranial flexure associated with eye position and long rostrum, loss of some external dewclaws, and extreme development of olfactory chambers and sinuses.

The close relationship of *Catagonus* and *Platygonus* does not necessarily indicate a phylogenetic continuity: A better understanding of the limits of *Prosthennops* and *Platygonus* is needed. If the limit of the genus *Platygonus* is restricted by the presence of non-molariform premolars, *Platygonus* and *Catagonus* must be considered to be sister groups, with *Prosthennops* containing a common ancestor.

Catagonus wagneri has survived as a component of the Chaco dispersal center (as used by Müller, 1973) along with other mammalian species such as the three-

banded armadillo *Tolypeutes matacus,* the greater pichiciego *Burmeisteria retusa,* the cricetid rodent *Pseudoryzomys wavrini,* and the mara *Dolichotis salinicola.* The growing literature on climatic and biotic fluctuations in South America and their possible correlation with the glacial cycles of the world has been recently summarized by Müller (1973), Haffer (1974), and Short (1975). Little is known of the history of the Chaco in the Pleistocene except that it also was subjected to xeric-mesic cycles that extended into postglacial times (Short, 1975:171). It is possible that in the Chaco, *Catagonus* and other arid-adapted plants and animals were afforded suitable habitats that were continuous with other nonforest centers during aridity cycles. Müller found, for example, strong affinities between the Chaco and the Brazilian Caatinga centers. His Pampa center has more affinities with the Chaco center than he presents, an example being the range of one of his indicator species, the hairy armadillo *Chaetophractus villosus.* This species is not confined to the Pampa center as recorded by Cabrera (1958:214) but, as we have found in our studies in Paraguay, occupies the Chaco center as well.

Such a speculative picture of Pleistocene ebb and flow of *Catagonus* populations should be tempered with an accounting for the isolation of *C. wagneri* in a single zoogeographic center. Some features suggest that the Chacoan peccary, evolving from larger ancestors of the Pleistocene, has become stunted. The large skull vs. the proportionally smaller body and the large, crowded premolars and molars vs. the short diastema and graeile skull may seem to support this hypothesis. Although our knowledge of this newly dis-

covered living relict is presently inadequate for this task, it is tempting to invoke either, or both, genetic drift in a restricted population (an islandic type of speciation) or severe selection toward a smaller-bodied *Catagonus* in a minimally adequate habitat. It is reasonable to suppose that in an earlier, more mesic cycle, the habitat for *Catagonus* was much more restricted than now. It is also reasonable to consider that its habitat may have been a rather unsatisfactory compromise between minimally adequate temperature, when the pampean grasslands to the south were no longer warm enough for peccaries, and the nearest available semi-open habitat—the thorn scrub of the Chaco.

In conclusion, *Catagonus wagneri* is a diurnal, cursorial animal, better equipped for far vision and speed for escape from predators than are the nocturnal *Tayassu. C. wagneri* is also an "olfactory" animal, utilizing an elaborate sinus system as a dust trap in the semi-arid environment to which it is restricted. Both preliminary stomach analyses and tooth structure indicate that *C. wagneri* is a browser, as compared with the more omnivorous *Tayassu. T. pecari* and *T. tajacu* have survival advantages over *C. wagneri* in having larger brains, either actually or proportionally, probably greater flexibility of diet, and shorter rostra affording greater flexibility of head positions without interference with forward vision. The three species of living peccaries meet in the Gran Chaco during what may be an interim period—the present—between a more arid cycle that favored thorn forest, steppe, and *C. wagneri,* and a moist cycle that will increasingly favor more mesic forests and *Tayassu.*

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